EAGLES AND EAGLE-LIKE VULTURES OF THE PLEISTOCENE OF RANCHO LA BREA

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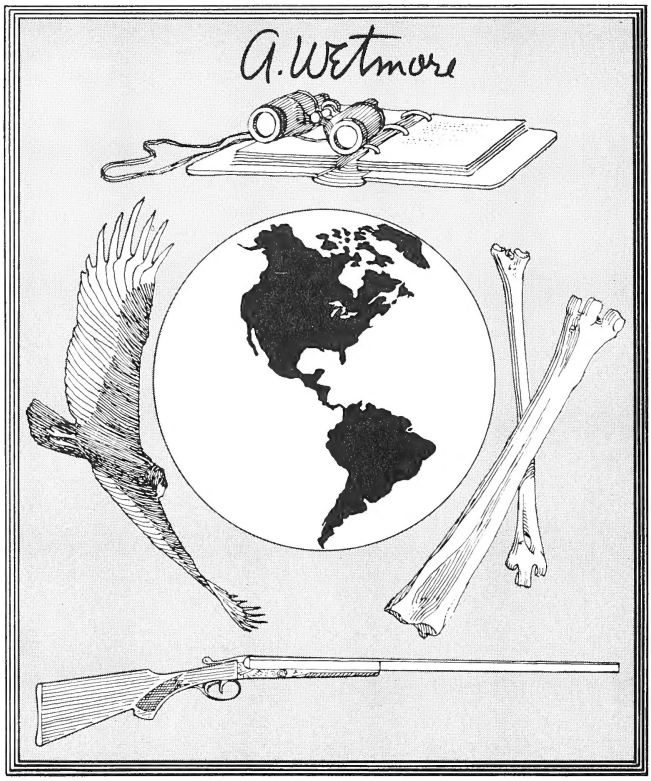

Alexander Wetmore

1946 *Sixth Secretary* 1953

A. Wetmore

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CONTRIBUTIONS TO PALÆONTOLOGY
FROM CARNEGIE INSTITUTION OF WASHINGTON

EAGLES AND EAGLE-LIKE VULTURES OF THE PLEISTOCENE OF RANCHO LA BREA

By HILDEGARDE HOWARD

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INTRODUCTION

One of the outstanding features of the Pleistocene avian assemblage of Rancho La Brea is the large representation of raptorial birds, particularly of the diurnal raptores, the Falconiformes. This group has been discussed and new species have been described by Dr. Loye Miller in a number of papers dating from 1909 to 1925.

Of the Falconiformes, the present paper is concerned only with the eagles and with the closely related group of vultures of old world affinities. The more remotely related New World Vultures, as well as the smaller hawks, and the falcons are not included. A list of the Rancho La Brea species to be considered, in the order of their presentation, follows:

[1]*Wetmoregyps daggetti* (Miller)
[1]*Urubitinga* (formerly *Geranoaëtus*) *fragilis* (Miller)
[1]*Morphnus woodwardi* Miller
Aquila chrysaëtos (Linnæus)
[1]*Spizaëtus* (formerly *Geranoaëtus*) *grinnelli* (Miller)
Haliæëtus leucocephalus (Linnæus)
[1]*Neogyps errans* Miller
[1]*Neophrontops americanus* Miller

Each of the extinct forms was described by Miller from the tarsometatarsus, and, with but few additions, this element represents our knowledge of these species up to the present time. It has been the author's aim, in the present study, to identify and describe all of the other principal skeletal parts of each species, and thus build up a concept of the entire bird. In two instances, a study of the skeleton as a whole has altered the generic assignment of the species; while in other instances, it has corroborated the testimony of the tarsometatarsus.

ACKNOWLEDGMENTS

It is a pleasure at this time to acknowledge indebtedness to those who have aided in this investigation.

Dr. Wm. Alanson Bryan, Director of the Los Angeles Museum, has made it possible for the writer to study the valuable collection of Rancho La Brea birds maintained at that Museum, upon which this work has been largely based.

Other institutions and individuals have kindly loaned specimens from their collections: American Museum of Natural History,

[1] Extinct.

California Institute of Technology, California Museum of Paleontology and Museum of Vertebrate Zoology, Santa Barbara Museum of Natural History, United States National Museum, Dr. Loye Miller and Mr. Donald R. Dickey.

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Others to whom the writer wishes to express her gratitude for their help and coöperation are Miss Lydia Bowen, Dr. J. A. Comstock, Dr. Joseph Grinnell, Mr. J. W. Lytle, Dr. Alden Miller, Dr. Chester Stock, Mr. George Willett, and Mr. H. A. Wylde.

The illustrations, with the exception of the text-figures, are reproductions of photographs made by Mr. H. Wm. Menke, and retouched by Mr. John L. Ridgway. Text-figure 1 was drawn by Mr. Ridgway, 2 and 3 by Mr. Henry Anson Wylde.

FOSSIL EAGLES FROM OTHER LOCALITIES

Fossil eagles have been reported from several localities in the United States beside Rancho La Brea, and from three geologic periods other than the Pleistocene. From the Eocene of Wyoming, Shufeldt has described two species of *Aquila*, *A. ferox* (Shufeldt, 1913b, p. 297) and *A. lydekkeri* (*op. cit.*, p. 298). The Miocene of Nebraska has yielded six species of eagles, or large hawks, namely: *Geranoaëtus ales* Wetmore (1926a, p. 403), *Geranoaëtus contortus* Wetmore (1923, p. 492), *Geranoaëtus dananus* (Marsh) (Marsh, 1871, p. 125, and Wetmore, 1926a, p. 405), *Buteo typhoius* Wetmore (1923, p. 489), *Urubitinga enecta* Wetmore (*op. cit.*, p. 500) and *Aquila* sp. (Wetmore, *op. cit.*, p. 504). Only one species is known from the Pliocene, and this, also, is from Nebraska: *Geranoaëtus conterminus* Wetmore (1923, p. 497).

In addition to the Pleistocene species recorded at Rancho La Brea, there are two species from Fossil Lake, Oregon, *Aquila pliogryps* Shufeldt (1891, p. 821) and *A. sodalis* Shufeldt (*loc. cit.*), one from Hawver Cave, California, originally designated as *Geranoaëtus* sp. (Miller, 1911b, p. 392), but herein described as a new species of the genus *Urubitinga* and one from Florida, *Geranoaëtus* sp. (Wetmore, 1931, p. 30).

Additional records for the Rancho La Brea species are as follows: *Wetmoregyps daggetti*, Carpinteria, California (Miller, 1931); *Urubitinga fragilis*, Carpinteria, California (Miller, 1931); *Aquila chrysaëtos*, McKittrick (Miller, 1922, p. 123) and Carpinteria, California (Miller, 1927b, p. 156), Fossil Lake, Oregon (Shufeldt, 1913a, p. 153),

Conkling Cavern, New Mexico (Howard, MS.); *Spizaëtus grinnelli*, Carpinteria, California (Miller, 1931); *Haliœëtus leucocephalus*, McKittrick (specimens in collection of California Institute of Technology), San Pedro (A. O. U. Checklist, 1931, p. 435), and Carpinteria, California (Miller, 1931), Fossil Lake, Oregon (Shufeldt, 1913a, p. 157), Sheridan County, Nebraska (Shufeldt, 1913b, p. 295), Conkling Cavern, New Mexico (Howard, MS.), several deposits in Florida (Wetmore, in Simpson, 1928, p. 3, and Wetmore, 1931, p. 30). The two species of Old World Vultures are known also from Carpinteria, California (Miller, 1927b, p. 156) and from McKittrick, California (*Neophrontops*, Miller, 1925a, p. 323; *Neogyps*, Miller, 1927a, p. 150).

SYSTEM OF CLASSIFICATION

The system of classification used in this paper is largely that of the fourth edition of the American Ornithologists' Union Checklist of North American Birds (1931), including the appended list of fossil birds. There are three instances, however, in which the writer has deviated from this list. These are: (1) the recognition of the subfamily Aquilinæ as distinct from the Buteoninæ; (2) the placing of the Old World Vultures after *Haliœëtus*; and (3) the inclusion of *Morphnus woodwardi* in the Buteoninæ, thus placing it ahead of *Aquila*, etc., in the list.

All of these changes were made for the sake of convenience in representing the taxonomic relations of the species here discussed as revealed by the characters under observation. The recognition of the subfamily Aquilinæ and the buteonine affinity of *Morphnus* follows Swann (1924–1926).

All species here discussed are included in the family Accipitridæ, under three subfamily heads: Buteoninæ, Aquilinæ and Ægypiinæ.

MATERIAL AVAILABLE

FOSSIL

For the most part, the Rancho La Brea fossil material herein described is in the collections of the Los Angeles Museum. The writer has had opportunity, also, while a student at the University of California to examine the collections there. Roughly estimated at least fourteen thousand specimens have been examined in the course of this study. Nearly two-thirds of this number are specimens of the Golden Eagle, *Aquila chrysaëtos*; *Haliœëtus leucocephalus* is second in abundance, its specimens including a little over 10 per cent of the total. Seven per cent of the specimens are of the extinct species, *Neophrontops americanus*, while the other extinct species run from about 4 per cent in *Neogyps* and *Spizaëtus grinnelli* to less

than one per cent in *Morphnus woodwardi*, and a very small fraction in *Wetmoregyps daggetti*.

The following elements of each species, with the exception of *Wetmoregyps daggetti*, were available: cranium, rostrum, mandible, sternum, furcula, coracoid, scapula, humerus, ulna, radius, carpometacarpus, pelvis, femur, tibiotarsus and tarsometatarsus. *Wetmoregyps* is represented, with certainty, by the tarsometatarsus and tibiotarsus only. The actual number of specimens of each element available for each species will be noted under the discussion of species.

With the exception of certain of the phalanges, no attempt has been made to identify any of the smaller, less characteristic elements. The segregation of the phalanges, however, did not prove altogether satisfactory; any reference that is made to the phalanges, therefore, can be considered as little more than speculation.

RECENT

The following skeletons of modern Accipitridæ were available for comparison:

Subfamily Buteoninæ

Heterospizias meridionalis: One complete skeleton; collection of U. S. Nat. Mus. No. 227378.

Geranoaëtus melanoleucus: Two complete skeletons; collection of L. H. Miller No. 233, and collection of U. S. Nat. Mus. No. 18471.

Buteo borealis: One complete skeleton; collection of L. A. Mus. No. 331. Eight incomplete skeletons; collection of L. H. Miller Nos. 139, 148, 152, 222, 240, 427, 446, 468.

Buteo regalis: One complete skeleton; collection of L. H. Miller No. 14. One incomplete skeleton; collection of L. A. Mus. No. 324.

Parabuteo unicinctus harrisi: One complete, one incomplete skeleton; collection of L. A. Mus. Nos. 245 and 100.

Asturina plagiata micrus: One complete skeleton; collection of Donald R. Dickey No. 17128.

Rupornis nattereri: Six furculæ, sterna, coracoids and scapulæ; collection of Amer. Mus. Nat. Hist. Nos. 159, 160, 161, 162, 163, 175.

Rupornis magnirostris griseocauda: One complete skeleton, collection of Donald R. Dickey No. 15586.

Busarellus nigricollis nigricollis: One complete skeleton; collection of Donald R. Dickey No. 17091.

Urubitinga urubitinga ridgwayi: Two complete skeletons; collection of L. H. Miller No. 738, and collection of Donald R. Dickey No. 17185.

Urubitinga anthracina anthracina: One complete skeleton; collection of Donald R. Dickey No. 15618.

Urubitinga anthracina subtilis: One complete skeleton; collection of Donald R. Dickey No. 16950.

Harpyhaliæëtus coronatus: Furcula, sternum, coracoids, scapulæ; collection Amer. Mus. Nat. Hist. No. 215.

Morphnus guianensis: Cast of tarsometatarsus; collection of L. H. Miller.

Harpia harpyja: One complete skeleton; collection of Amer. Mus. Nat. Hist. No. 1383. One cast of tarsometatarsus; collection of L. H. Miller.

Subfamily Aquilinæ

Aquila chrysaëtos: Six complete skeletons; collection of L. H. Miller Nos. 679, 923, 926, 927, collection of Calif. Mus. Vert. Zool. No. 50475, and collection of L. A. Mus. No. 468. Seven incomplete skeletons; collection of L. H. Miller Nos. 421 and 471, collection of Calif. Mus. Vert. Zool. Nos. 41410 and 42686, and collection of L. A. Mus. Nos. 3, 4 and 5.

Spizaëtus ornatus: Two incomplete skeletons; collection of Donald R. Dickey Nos. 16872 and 16929.

Haliæëtus leucocephalus: Two complete skeletons; collection of Donald R. Dickey No. 22944, and collection of Calif. Mus. Vert. Zool. No. 8326. Three incomplete skeletons; collection of L. H. Miller No. 626, and collection of L. A. Mus. Nos. 32 and 291.

Subfamily Ægypiinæ

Gypaëtus barbatus: One complete skeleton; collection of L. H. Miller No. 263.

Sarcogyps calvus: One complete skeleton; collection of L. H. Miller No. 226.

Neophron percnopterus: Two complete skeletons; collection of L. H. Miller No. 227, and collection of L. A. Mus. No. 239 (the latter skeleton mounted).

Species?[1] One complete skeleton; collection of L. A. Mus. No. 232.

In addition to the specimens listed above, representative genera of each of the other subfamilies of the Accipitridæ were examined.

To avoid constant repetition in the descriptions to follow, it should be understood that wherever fossil species are said to resemble or not to resemble existing species, the writer is referring only to the specimens of existing species listed above. In nearly all instances there are more fossil specimens of a species than there are Recent specimens for comparison. Where the fossil forms are found to vary individually, a variation must be allowed for in the related Recent forms, though perhaps less than is encountered in the fossil species, in which the range of variation is great.

METHODS OF IDENTIFICATION OF MATERIAL

Among the specimens of raptorial birds contained in the Los Angeles Museum collection, the various skeletal elements of *Aquila chrysaëtos* and *Haliæëtus leucocephalus* were easily detected and segregated before attempting the identification of the six extinct species.

Since each of the extinct species considered here has been described from a tarsometatarsus dissociated from all other elements of the skeleton, the identification of the other bones presented what seemed at first a hopeless undertaking. However, after a careful study it became evident that each element could be segregated as to species on the basis of diagnostic characters similar to those employed in separating the tarsometatarsi. The Los Angeles Museum collection offers unusual advantages for attacking a problem of this kind. With so large a number of specimens, individual variations within

[1] This skeleton was bought from Ward's Natural Science Establishment labeled *Haliæëtus leucocephalus*. It is, however, undoubtedly an Old World Vulture, though the species can not be determined by comparison with the specimens at hand.

a species can be observed as such, and the possibility of mistaking them for specific characters is practically eliminated. Even in this collection, however, *Wetmoregyps* is very sparsely represented; the most abundant of all elements, the tarsometatarsus, numbering but four in this form. Owing to the scarcity of *Wetmoregyps*, and perhaps also to a resemblance of this form to other representatives of the buteonine subfamily in the less characteristic elements of the skeleton, it has been found possible to segregate most of the skull and skeletal structures into but five groups; *Wetmoregyps* is known with certainty only from the tarsometatarsus and tibiotarsus, already figured by Miller (1925, pl. 5, figs. F, G, H) with the possible addition of certain of the phalanges.

Having subdivided the original collection of particular elements into rather well-defined groups, the task of bringing the groups for each element together in their proper associations was less arduous than might be supposed. The method by which this was accomplished, or at least by which we believe it has been accomplished, the writer has endeavored to set forth in the following paragraphs.

In general, identification has been based upon four sources of information, which in order of importance, are: (1) resemblance to modern species, as compared with the tarsometatarsi; (2) resemblance to other Rancho La Brea fossil species, also as compared with the tarsometatarsi; (3) size; (4) relative abundance.

It is difficult to state in what order the criteria employed in recognizing the separate elements were applied, for after all elements were gone over, each structural part was considered in its interrelations with the other parts of the skeleton. In general, however, the tarsometatarsus was taken as a basis to which were added the remaining leg elements. The wings and pectoral girdle were studied together and then associated with the legs. The skull and mandible were added last.[1]

Tarsometatarsus

The tarsometatarsi (described and recorded by Miller, 1911a, 1915 and 1916) represent eight species, *i.e. Wetmoregyps daggetti, Morphnus woodwardi, Urubitinga* (formerly *Geranoaëtus*) *fragilis, Spizaëtus* (formerly *Geranoaëtus*) *grinnelli, Aquila chrysaëtos, Haliæëtus leucocephalus, Neogyps errans, Neophrontops americanus.* Omitting the modern species, *Aquila chrysaëtos* and *Haliæëtus leucocephalus*, the resemblance of these tarsometatarsi to modern species, to each other, their size and abundance are given below.

[1] As a further check on the identifications of the Rancho La Brea species, the writer has recently been able to study the eagle bones in the collections of the Santa Barbara Museum of Natural History and the California Institute of Technology from the Carpinteria and McKittrick asphalt deposits. Since all of the species present at Rancho La Brea are not represented in these other deposits, and those that are occur in different proportions, it was possible by comparing the three collections to verify the identifications of the various elements.

Group	Species	Resemblance modern forms	Resemblance fossil forms	Size			Abundance
				Length	Breadth[1]		
					prox.	dist.	
				mm.	*p. ct.*	*p. ct.*	*specimens*
1	Wetmoregyps daggetti	Buteoninæ (Urubitinga)	U. fragilis M. woodwardi	167	11.8	13.6	4
2	Urubitinga fragilis	Buteoninæ (Urubitinga)	M. woodwardi W. daggetti	113–96	16.2	18.6	126
3	Morphnus woodwardi	Buteoninæ (Geranoaëtus and Morphnus)	U. fragilis W. daggetti	140–125	17.5	20.0	36
4	Spizaëtus grinnelli	Aquilinæ (Spizaëtus)	.....	114–100	17.2	19.5	171
5	Neogyps errans	Ægypiinæ Haliæëtus	.....	93–84	22.4	25.6	122
6	Neophrontops americanus	Ægypiinæ (Neophron)	.....	97–85	15.7	16.6	211

[1] Average breadths of proximal and distal ends relative to length.

Tibiotarsus

The tibiotarsus, also, could be divided into six groups on the same bases as the tarsometatarsus.

Group	Species	Resemblance modern forms	Resemblance fossil forms	Size			Abundance
				Length	Breadth[1]		
					prox.	dist.	
				mm.	*p. ct.*	*p. ct.*	*specimens*
1	Wetmoregyps daggetti	Buteoninæ (Urubitinga)	U. fragilis M. woodwardi	215	....	9.8	1
2	Urubitinga fragilis	Buteoninæ (Geranoaëtus)	M. woodwardi W. daggetti	149–130	12.0	12.1	44
3	Morphnus woodwardi	Buteoninæ (Geranoaëtus)	U. frægilis W. daggetti	190–171	12.5	12.7	12
4	Spizaëtus grinnelli	Aquilinæ (Spizaëtus)	.....	164–150	12.4	12.0	59
5	Neogyps errans	Ægypiinæ	.....	153–140	13.9	13.4	47
6	Neophrontops americanus	Ægypiinæ (Neophron)	.....	124–109	12.2	11.9	99

[1] Average breadths of proximal and distal ends relative to length.

Femur

With the femur, only five groups could be distinguished. No femur was found which would correspond with the long, slender tarsometatarsus and tibiotarsus of *W. daggetti*. On the basis of the same criteria applied to the other leg elements, the five represented groups were assigned to the other five species.

Group	Species	Resemblance modern forms	Resemblance fossil forms	Size			Abundance
				Length	Breadth[1]		
					prox.	dist.	
				mm.	*p. ct.*	*p. ct.*	*specimens*
1							
2	Urubitinga fragilis	Buteoninæ	M. woodwardi	107–95	19.0	15.7	32
3	Morphnus woodwardi	Buteoninæ	U. fragilis	130–124	20.4	16.8	7
4	Spizaëtus grinnelli	Aquilinæ	.....	121–112	22.0	16.8	40
5	Neogyps errans	Ægypiinæ and Haliæëtus	.....	113–103	22.8	17.5	39
6	Neophrontops americanus	Ægypiinæ (Neophron)	.....	83–71	23.9	17.6	109

[1] Average breadths of proximal and distal ends relative to length.

The identification of the remaining elements of the skeleton presented a slightly different problem than the identification of the leg bones. Aside from the fact that only five groups were evident, as was also the case with the femur, the size of the bones differed as well. Whereas in the leg bones, excepting the few specimens of *W. daggetti*, there was but one group of large-sized bones for each element (this group assignable to *Morphnus woodwardi*), in the other elements, the large bones fell into two groups. One group was buteonine in character and was assigned to *Morphnus woodwardi*. The other, it was logical to suppose, must be assigned to one of the short or slender-legged species, the only alternative being assignment to a species not represented by leg bones, resulting in the presence of two species, one consisting only of legs, the other being legless. This alternative, it is needless to say, is wholly illogical, particularly in view of the abundance of tarsometatarsi; any species well represented by other structural parts could safely be assumed to be as well or better represented by the tarsal element. Assuming these larger bones to have been associated with legs of smaller size, it was necessary to determine which of the represented species could properly be expected to have had relatively weak legs, with a large body and large wings. Among the subfamilies of the Accipitridæ, this combination of characters exists in the Ægypiinæ. *Neophrontops* was immediately discarded as a possibility, since its skeletal parts were readily identified by their similarity to *Neophron*, and the bones in question were assigned to *Neogyps*. This assignment was further justified by careful study of the individual elements revealing, in many instances, similarities to the vultures, and to *Haliœëtus*. The evidence bearing on each separate element is discussed below.

Pelvis

Of the five groups into which the pelves could be divided, two consisted of large specimens, two of medium size and one small. The small group was recognizable as *Neophrontops* by its general similarity to *Neophron*. One large and one medium group showed resemblance to the Buteoninæ and were assigned to *Morphnus* and *Urubitinga*, respectively. The other large and medium groups were assigned to *Neogyps* and *Spizaëtus*, respectively, on the basis of the following characters; (1) though the femur of *Neogyps* is small, the head is relatively large, and this larger head would not fit properly into the small acetabulum of the small pelvis, while the narrow head of the femur of *Urubitinga fragilis* was too small for the large acetabulum; (2) the large pelvis shows characters intermediate between *Haliæëtus* and the Ægypiinæ, which is the case also with the tarsometatarsus of *Neogyps*, while the small pelvis bears the resemblance to the Aquilinæ which characterizes the tarsometatarsus of *grinnelli*.

Sternum

With the size of the pelvis of each species decided upon, the sternum was not difficult to identify, since the pelvis and sternum in general agree in size. As with the pelvis, the characters, also, correspond.

Group	Species	Resemblance modern forms	Size	Abundance
1				
2	Morphnus woodwardi	Buteoninæ	Large	2 spec.
3	Urubitinga fragilis	Buteoninæ	Medium	11
4	Spizaëtus grinnelli	Aquilinæ (Spizaëtus)	Medium	12
5	Neogyps errans	Ægypiinæ	Large	17
6	Neophrontops americanus	Ægypiinæ (Neophron)	Small	42

Furcula and Coracoid

The furcula and coracoid presented no outstanding difficulties, by reason of their agreement with the tarsometatarsus in the matter of similarities with living forms. The coracoids of group 6 present one exception; but though individual in characters, they were assigned to *Neophrontops* on the basis of small size and relative abundance.

Group	Species	Resemblance modern forms		Size, both elements	Abundance	
		Furcula	Coracoid		Furcula	Coracoid
1						
2	Urubitinga fragilis	Buteoninæ	Buteoninæ	Medium	13	58
3	Morphnus woodwardi	Buteoninæ	Buteoninæ	Large	6	12
4	Spizaëtus grinnelli	Spizaëtus	Spizaëtus	Medium	17	58
5	Neogyps errans	Haliæëtus and Ægypiinæ	Ægypiinæ	Large	25	37
6	Neophrontops americanus	Neophron	.....	Small	33	172

SCAPULA

In the scapula, the characters indicative of subfamily relationship are less clearly defined. The two groups containing the larger specimens were identified as *M. woodwardi* and *Neogyps errans*, each group being assigned to its respective species on the basis of relative abundance[1]—*woodwardi* having only 8 specimens, *errans* 44—and the resemblance of the one group (assigned to *M. woodwardi*) to the Buteoninæ, of the other (assigned to *N. errans*) to *Gypaëtus* in certain characters. *Neophrontops* was identified by its small size and similarity to *Neophron*. The separation of *fragilis* and *grinnelli* was made on the basis of greater similarity of the former to the Buteoninæ, of the latter to the Aquilinæ.

HUMERUS

Group 5 was set aside as *Neogyps errans* because of the large size of the bones, corresponding to the large body bones, and because of the number of specimens being too great to be classified with *Morphnus woodwardi*; careful study also revealed certain characters resembling *Haliæëtus* and the Ægypiinæ. *Neophrontops* was identified by its general resemblance to *Neophron*, its abundance, and its small size. Difficulties arose with respect to *M. woodwardi*, *U. fragilis* and *S. grinnelli*. In the tarsometatarsus, it has been noted that *woodwardi* and *fragilis*, though exhibiting distinct specific characters other than size, show certain resemblances to each other as distinguished from any of the other species; probably subfamily characters. Group 4, though possessing characters closer to *Spizaëtus* than is true of any of the other groups, presented certain difficulties with regard to size. In this group there are three large specimens, which are 10 mm. greater in length than the maximum of the remain-

[1] Though the criterion of relative abundance can not be safely applied where the difference in occurrence is slight, its application is considered practical here, in view of the great discrepancy in the abundance of the two species, not only in this element but in the tarsometatarsus and other elements of the skeleton where identification is based on other criteria.

ing eleven complete specimens. These two sizes of group 4 are, however, similar in other characteristics. On the other hand, those specimens which have been placed in groups 2 and 3 are divided by 19.2 mm. in length and, though similar in general characters, possess certain points of distinction; furthermore, the specimens in group 3 attain a greater maximum in size than is true of the largest specimens of group 4. Thus groups 2 and 3 have been identified as *Urubitinga fragilis* and *Morphnus woodwardi* respectively, while the two sizes of group 4 (possessing no distinction other than size) are placed with *Spizaëtus grinnelli*.[1]

Group	Species	Resemblance modern forms	Resemblance fossil forms	Size: Length	Abundance
				mm.	*specimens*
1					
2	Urubitinga fragilis	Buteoninæ	Morphnus woodwardi	173–158	42
3	Morphnus woodwardi	Buteoninæ	Urubitinga fragilis	217–193[a]	12
4	Spizaëtus grinnelli	Closest to Spizaëtus		173–142	45
5	Neogyps errans	Ægypiinæ and Haliæëtus		217–202	64
6	Neophrontops americanus	Neophron		148–134	133

[a] Extremes in length of humerus of *M. woodwardi* were estimated from broken specimens.

Ulna

In this element the two groups of large bones were identified primarily on the basis of relative abundance: *Neogyps* with 60 specimens, *Morphnus* with 8. In corroboration of this segregation, the group assigned to *Neogyps* was found to exhibit characters similar to the Ægypiinæ. *Neophrontops* was distinguishable by its small size and resemblance to *Neophron*. *Urubitinga fragilis* and *Spizaëtus grinnelli* were separated on the basis of greater resemblance of the former to the Buteoninæ, of the latter to the Aquilinæ.

Radius

The radius has always proven an unsatisfactory bone for purposes of classification, and in the present study it has been the most difficult element to identify. The characters of the distal end were not found to be sufficiently outstanding to permit the element to be classified by that portion. The specimens under consideration have, therefore, been identified on the basis of the proximal end only (*Neophrontops*, is, however, an exception, for in this genus the entire element serves to distinguish the form from any other accip-

[1] It may be noted here that examination of modern specimens of *Aquila chrysaëtos* has revealed greater variation in size of humerus and other wing bones than is true of the leg bones.

itrid). In the larger forms, no complete specimens are available. The proximal ends fall into two groups, one with five specimens, the other with six; those of the former group exhibit characters similar to the Buteoninæ, and have been assigned to *Morphnus woodwardi*; those of the latter are vulture-like in certain respects and are identified as *Neogyps errans*. *Neophrontops* is identifiable because of its small size and similarity to *Neophron*. *Urubitinga fragilis* and *Spizaëtus grinnelli* are distinguishable on the basis of closer resemblance of the former to the Buteoninæ, of the latter to the Aquilinæ. There are a few specimens of proximal end which do not appear to accord with the specimens of any of the above groups. These bones, however, do not constitute a group in themselves, but differ from each other; it is not feasible to consider them as distinct species in view of the immense amount of variation which is known to exist in the characters of the radius and the few radii available in the collection. Possibly one of the bones belongs with *Wetmoregyps daggetti*, the others are probably variants of the groups already identified.

Carpometacarpus

Groups 2 and 3 were identified as *U. fragilis* and *M. woodwardi*, respectively, because of the general similarities between the two, as well as a general resemblance to the Buteoninæ. Group 5 was identified as *Neogyps errans* because of its large size (distinguishing it from all others except *Morphnus*) and relatively great abundance (distinguishing it from *Morphnus*). Group 6 was assigned to *Neophrontops* because of its small size and great abundance. Group 4 was assigned to *S. grinnelli* since its characters are closest to the Aquilinæ. In minimum size *grinnelli* overlaps the maximum of *Neophrontops*, but it attains even greater maximum length than *fragilis*; this unusual range in size was noted also in the humerus ascribed to *grinnelli*.

Skull and Mandible

In no case have the skull and lower mandible been found associated. In the Los Angeles Museum collections from Rancho La Brea, no complete skull (cranium and rostrum together) is available. However, in one group of medium-sized individuals (this group assigned to *Urubitinga fragilis*), there are two instances in which the cranium and rostrum of one individual, though broken apart, may be fitted together. A complete skull of a large extinct accipitrid has been found in the Carpinteria asphalt deposit. Through the kindness of Dr. Loye Miller, who is studying the birds from these beds, the present writer has had the opportunity of examining this specimen. It was found that certain crania and rostra in the Los Angeles Museum collection which had been set aside as belonging together (assigned to *Neogyps errans*) corresponded to the cranium and ros-

trum of this complete specimen. With one set of large crania and rostra thus accounted for, it seemed only proper that the remaining large rostra should belong with the remaining crania of large size, and similarly that with one set of medium-sized specimens definitely associated, the remaining crania and rostra of medium size should be grouped together. There was no possibility of confusion of the cranium and rostrum of *Neophrontops* with any of the other accipitrids.

The mandibles were identified by relative abundance (agreeing with the skulls in this respect) as well as resemblances to modern species.

The cranium, rostrum and mandible of *M. woodwardi* were so identified on the basis of large size and rarity. Those of *Neogyps errans* were so classified because of large size and abundance. Of the two groups of medium size, the number of crania is the same for each, and the discrepancy in numbers of rostra and mandibles is not marked. Identification here was made on the basis of close resemblance of the three elements of one group to the Buteoninæ (*U. fragilis*) and of the other to the Aquilinæ (*S. grinnelli*). In the crania of *Neophrontops* there are certain points of resemblance to *Coragyps atratus*. However, the absence of basipterygoid processes precludes the possibility of their belonging to the Cathartidæ; furthermore, a good series of crania, closely resembling *C. atratus*, has been assigned by Miller to the Rancho La Brea Pleistocene representative of the genus *Coragyps*, *C. occidentalis* (Miller). The specimens of *Neophrontops* can readily be distinguished both from the fossil *C. occidentalis* and from *C. atratus*. The rostrum and mandible of *Neophrontops* were easily identified because of their resemblance to *Neophron*.

There are a few specimens (other than the distal ends of radii, which in most cases could not be safely classified) the identity of which is questioned; these are: 5 proximal ends of radii (divided into three groups); 1 articular end of scapula; 2 distal ends of humeri.

Some of these specimens may belong to *Wetmoregyps*; on the other hand, they may all be variants of some of the other species already identified. The possibility of the presence of another species, unrepresented by the tarsometatarsus, as we have said before, is remote; there are more than twice as many tarsometatarsi as of any other single element; furthermore, there is no general resemblance of these unidentified elements to any one group, and the specimens may in all probability belong to several different species.

DISCUSSION OF SPECIES

In the following paragraphs, the writer has endeavored to set forth the characters of each individual element of the five extinct species under consideration, as well as to present a somewhat general statement of the fossil representation of the two species still in existence.

The discussion of the individual elements has been written with two purposes in view, namely (1) to point out all characters which the writer has observed to be of value in identifying the various elements of each species, and (2) to indicate those characters which appear to be of genetic importance, relating the fossil to a certain subfamily or genus.

It has been evident to the writer in the course of this study that some features of certain elements are of greater taxonomic value than others.

Subfamily diagnostics were particularly manifested in the following characters:

1. Head of coracoid.
2. Posterior arch of pelvis.
3. Proximal end of femur.
4. General shape of tarsometatarsus and character of hypotarsus.
5. Distal end of tibiotarsus, particularly intercondylar groove in distinguishing the Aquilinæ from the Buteoninæ.
6. Characters of the ventral manubrial spine and the sternocoracoidal impression of the sternum.

Generic and specific characters were more difficult to observe and were found to vary in different groups.

Apparently the cranium (at least when stripped of the vomer, palatines and pterygoids, which are lacking in the specimens from the asphalt), does not contain characters of importance in determining relationship within the three subfamilies considered. The absence of the basipterygoid processes in the accipitrids, as contrasted with their presence in cathartids, however, was a helpful point in the study of *Neophrontops*.

The importance of the other elements of the skeleton in identification varied somewhat, depending on the group. There was no element, however, which was entirely valueless throughout. In general, the wing bones were found to be less diagnostic and more variable than the leg bones; this applied to variation in size as well as to structural details, for the range in size in the wing elements in several instances was found to exceed that of the leg bones.

The names applied to the various parts of each element follow the system outlined in a series of labeled figures in Howard (1929, pp. 314–325, figs. 1–54).

SUBFAMILY BUTEONINÆ

In the subfamily Buteoninæ are included *Wetmoregyps daggetti*, *Urubitinga fragilis* and *Morphnus woodwardi*.

The differences which exist between species of one genus in this subfamily, as well as the similarities which may be noted between genera, cause considerable difficulty in the assignment of a fossil

species to its proper genus. In comparing the fossils at hand, it was possible to eliminate all but six of the existing genera of buteonines of which specimens were available for study. The six whose characters agree in some respects with the fossil specimens are: *Heterospizias*, *Geranoaëtus*, *Buteo*, *Urubitinga*, *Harpyhaliœtus* and *Morphnus*.

Unfortunately, only the tarsometatarsus of *Morphnus*, and the shoulder girdle of *Harpyhaliœtus* are available. In the other five genera, in which the entire skeleton could be studied, it was obvious that but few characters could be considered constant within a genus; more constancy was noted within a species. The most important characters of generic significance were found to be those of the rostrum and pelvis. Disregarding these, any other element by itself was of but little value as a generic indicator, though when the skeleton was taken as a whole, the same tendencies appearing in various elements aided in generic determination.

Wetmoregyps daggetti (Miller)

Plate 13

Morphnus daggetti Miller, Condor, **17**, 179–181, figs. 63, 1915.
Wetmoregyps daggetti (Miller), Condor, **30**, 255–256, 1928.

This species was described from a tarsometatarsus in the collections of the Los Angeles Museum. Since the original description, three more tarsometatarsi (only one of which is complete) and an almost complete tibiotarsus have been identified and discussed by Miller (1925b). In the present study, the writer has been able to add almost nothing to the knowledge of this species.

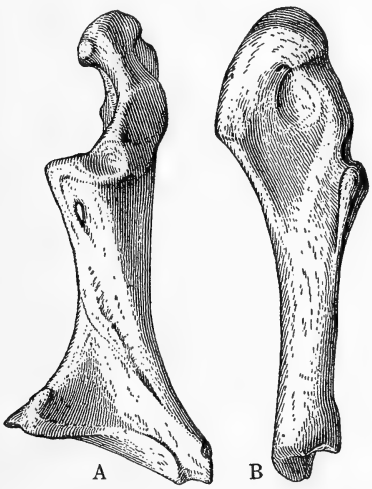

Fig. 1—Coracoid of *Wetmoregyps daggetti*, L. A. M. No. D1217. Natural size. A, posterior view; B, internal view.

Single specimens of phalanx 1 of digits 1 and 3 have been tentatively assigned to *Wetmoregyps*. In each phalanx the size is intermediate between specimens which are believed to belong with *Morphnus woodwardi*, and others which are thought to belong with *Urubitinga fragilis*, and the characters are, in general, similar to both species.

The distal portions of both the tibiotarsus and tarsometatarsus of *Wetmoregyps* very closely resemble (both in size and physical characters) specimens of these elements assigned to *Morphnus woodwardi*, though of course the extreme length of the bones as well as the character of the proximal end and of the shaft in the tarsometatarsus immediately distinguish them from *M. woodwardi* when the complete elements are compared (the proximal end of the tibiotarsus of *Wetmoregyps* is broken so that its characters are not known). Considering the similarities of the two species as shown in the leg bones, it is perhaps possible that other elements of the skeleton are also similar in certain characters, and that among the fragmentary specimens now assigned to *M. woodwardi* there are

bones belonging to *Wetmoregyps*. In fact it is even possible that some elements may have been confused with the smaller buteonine species, *Urubitinga fragilis*, if *Wetmoregyps* parallels *Urubitinga urubitinga* in body proportions as it does in the relative slenderness of the long leg bones.[1]

Urubitinga fragilis (Miller)

Plates 1 to 6

Geranoaëtus fragilis Miller, Univ. Calif. Publ. Bull. Dept. Geol., **6**, 315–316, figs. 5a-5b, 1911.

This species was described from a tarsometatarsus in the collections of the University of California. Though other specimens of this element have been found, both in the University collections and in those of the Los Angeles Museum, no other elements of the skeleton have been identified until the present time.

With all of the principal skeletal elements now available, the species has been studied in detail, and its relationships noted, both with regard to separate elements and to the skeleton as a whole. Each element studied has added to the conviction that *fragilis* is not a species of genus *Geranoaëtus*, but shows closer affinity with *Urubitinga* or *Heterospizias*. It should be noted here that Wetmore (1923, p. 502) suggested the possibility of relationship of *fragilis* with *Urubitinga*, basing his suggestion on "the slender form and high location of the tubercle for the tibialis anticus seen in the metatarsus."

The idea of assigning *fragilis* to a new genus is not considered, in view of the complexity of similarities and variations of the genera already existing within the subfamily Buteoninæ. A new genus would only add to the complexity while contributing nothing of value to the taxonomy of the group. A detailed description of the species follows.

Skull

Plate 1, figs. 1–2

Material available—Two, cranium with rostrum (found dissociated but can be fitted together); five crania; four rostra.

Characters—A relatively long and narrow skull; length between small *Geranoaëtus melanoleucus* on the one hand and large *Buteo regalis* on the other, but narrower across postorbital processes than either. Agreeing in relative breadth with *Urubitinga urubitinga* and *U. anthracina* (about 55 per cent of total length of skull). Rostrum long and narrow, agreeing in greatest breadth of palate relative to length with *Urubitinga; Heterospizias* next in breadth, and *Buteo* and *Geranoaëtus* decidedly broader. Maxillo-palatines close together, with no space between.

Mandible

Plate 1, fig. 3

Material available—Two complete; one left ramus with symphysis; two, half of left ramus.

Characters—Showing same character of length and narrowness as noted in skull. Closest to *Urubitinga*.

[1] Since the above writing, the author has had the opportunity of studying the eagle remains from the Carpinteria asphalt deposits. At this locality *Wetmoregyps daggetti* occurs in greater abundance than at Rancho La Brea and it was therefore possible to identify several of its skeletal elements. This study has resulted in the discovery of a coracoid in the Rancho La Brea collection which can be assigned to *daggetti*. The bone is similar in size and in general characters to a large individual of *Urubitinga fragilis*, but differs in certain aspects of the head region, particularly in the character of the pneumatic foramen, which in *daggetti* is scarcely more than an irregular depression adjacent to the furcular facet; the specimen had been set aside as a possible variant of *fragilis*. The bone measures 57.3 mm. in length and 20 mm. in breadth of head. Two views of this specimen are shown in text-figure 1. The assignment of this element to *Wetmoregyps*

STERNUM

Plate 2, figs. 1 and 1a

Material available—Five nearly complete; five incomplete.

Characters—Sterno-coracoidal impression evenly margined and tending to be long and narrow; intermuscular lines longer than in *Geranoaëtus* and tending to be straight, or concave outwardly; xiphial area moderately broad and clearly marked, particularly at junction with carina—the carina and sternal plate are slightly depressed at this point and the xiphial area protrudes laterally beyond the carina and under the sternal plate.

Size—Length about as in small *Geranoaëtus melanoleucus*.

FURCULA

Plate 1, figs. 4 and 4a

Material available—One complete; two left, one right clavicle with symphysis; three left, five right clavicle.

Characters—More rounded than oval in shape, as in all genera under consideration; dorsal ends broad and only slightly raised on inner side, somewhat resembling *Buteo, Heterospizias*, or *Geranoaëtus*, and to a less extent *Urubitinga anthracina* (*U. anthracina* and *U. urubitinga* differ as markedly in this character as either differs from any of the other genera, and therefore the character is not given much weight as a generic indicator); outer edges of clavicles thin and tending to turn backward as in *Buteo, Geranoaëtus* and *Urubitinga;* intermuscular lines of posterior side close to outer margin of clavicles as in *Heterospizias* and *Urubitinga* (near center or internal margin in *Geranoaëtus* and *Buteo*); furcular process well developed posteriorly; ventral border of symphysis bluntly pointed, and tending to protrude downward and backward (this character distinctive in *fragilis*).

Size—Slightly larger than large *Buteo regalis;* smaller than *Geranoaëtus melanoleucus*.

SCAPULA

Plate 1, figs. 5–5b

Material available—Twenty-four specimens.

Characters—Acromion more developed anterodorsally than in most of the Buteoninæ, but similar to *Urubitinga anthracina;* similar to *Urubitinga anthracina* also in straight ventral (outer) margin of glenoid facet and angular junction with shaft distally and head proximally; *Buteo, Heterospizias* and *Harphyhaliætus* have straight margins but differ in other characters from *fragilis; Geranoaëtus* and *Urubitinga urubitinga* have rounded margins and differ in other characters as well. Since *U. anthracina* and *U. urubitinga* differ so markedly in the characters of this element, the importance of the similarity of *fragilis* to *anthracina* may be questioned. However, since the resemblance holds for more than one character of the element, it would seem that the similarity is not merely a coincidence.

CORACOID

Plate 2, figs. 2–2b

Material available—Twenty-six right; twenty-nine left.

Characters—Furcular facet buteonine in the absence of a distinct distal margin. Character of internal side of head somewhat similar to *Harpyhaliætus* and *Heterospizias* in the fairly even contour of the furcular facet, and in the absence of small pneumatic openings, and to *Heterospizias* but not *Harpyhaliætus* in the close proximity of the well-developed, larger pneumatic foramen to the posterior edge of the facet.

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daggetti establishes the proportions of that species as closely paralleling those of *Urubitinga urubitinga*. Of all the elements of *Wetmoregyps* represented in the Carpinteria collection, the coracoid is the only one which may be added to the Rancho La Brea list. This specimen was not included in the discussion on pages 4 and 6.

Contour of facet slightly more uneven in *Urubitinga*, still more so in *Geranoaëtus*. Small pneumatic openings present in *U. urubitinga* and *Geranoaëtus*, but not in *U. anthracina;* larger pneumatic opening well developed in *U. anthracina* and *Geranoaëtus*, but not in *U. urubitinga*. Anterior end in external aspect longer and narrower than *Geranoaëtus*, *Harpyhaliætus*, or *Heterospizias;* closer to *Urubitinga*. Also differing from *Heterospizias* in greater rugosity of this external surface.

Size—Height: 59.5 mm. to 51.9 mm., average 55.1 mm. Distance from sternal facet to procoracoid, relative to height, approximately 61.8 per cent.

Humerus

Plate 3, figs. 1 and 1a

Material available—Six complete; three lacking proximal end; one lacking distal end; twenty-four proximal end; eight distal end.

Characters—Long, slender bone with relatively short deltoid crest and comparatively straight shaft; resembling *Heterospizias* and *Urubitinga urubitinga* in these characters, though longer. Contour of margin of deltoid crest uneven as in *U. urubitinga; Heterospizias* and *U. anthracina* even. Bicipital crest rounded. In *Geranoaëtus* a heavier, more curved bone with longer deltoid crest, and bicipital crest more square.

Measurements of Humerus

Specimen	a Length	b Breadth of proximal end	c Length of deltoid crest	Ratio of b to a	Ratio of c to a
	mm.	*mm.*	*mm.*	*p. ct.*	*p. ct.*
Heterospizias U. S. Nat. Mus. No. 227378	119.0	20.7	42.0	17.3	35.2
Geranoaëtus U. S. Nat. Mus. No. 18471	145.0	28.3	58.4	19.5	40.6
Geranoaëtus L. H. Miller No. 233	160.0	32.0	61.8	20.0	38.6
U. urubitinga L. H. Miller No. 738	120.8	21.9	43.6	18.1	36.0
U. urubitinga D. R. Dickey No. 17185	119.1	20.6	41.7	17.3	35.0
U. anthracina D. R. Dickey No. 16950	105.3	19.6	41.9	18.6	39.7
15618	109.5	19.7	41.7	18.0	38.0
fragilis[1] L. A. Mus. No. C8735	159.3	29.9	58.7	18.7	36.8
D8248	165.1	30.5	59.6	18.4	36.0

[1] Extremes of length in *fragilis*, 173.9–158.2 mm.; average 165.2 mm.

The curvature of the humerus appears to be of significance; *Buteo* and *Geranoaëtus* are strongly curved, while *Heterospizias* and *Urubitinga* are straighter; *Urubitinga anthracina* is less straight than *U. urubitinga* but straighter than *Buteo* or *Geranoaëtus*.

With respect to curvature of shaft and short deltoid crest, *fragilis* is in general agreement with *Urubitinga enecta* Wetmore from the Miocene of Nebraska. This species has been figured by Wetmore (1923, p. 203, figs. 17 and 18) and the present writer has used these figures in comparing *fragilis* with *U. enecta*. The larger specimens

of *fragilis* are approximately equal in size to *U. enecta*. *Fragilis* may be distinguished from the Miocene form, however, by the shape of the ectepicondylar prominence and by less excavation of the impression of the brachialis anticus and the area distal thereto, as well as of the shaft of the bone on the anconal side of the proximal end.

Ulna

Plate 4, figs. 1–1b

Material available—Two complete; ten proximal half; thirteen distal half.

Characters—Distinct pit-like depression present between olecranon and external cotyla as in *Buteo* and *Urubitinga*, and to a less extent *Geranoaëtus melanoleucus;* humero-ulnar depression shallow; olecranon similar to *Geranoaëtus*, blunt and of medium height, higher than *Heterospizias* and lower and less pointed than *Urubitinga*.

Size—Bone long and slender. Length equaling or exceeding that of *G. melanoleucus: fragilis*, 201.2 mm. and 182.1 mm.; *G. melanoleucus*, 189.4 mm. and 166.2 mm.

Radius

Plate 4, figs. 2 and 2a

Material available—One complete; two proximal half.

Characters—Ligamental papilla elongated; capital tuberosity prominent and thin, closest to *Buteo* and *Urubitinga; Heterospizias* and *Geranoaëtus* heavier.

Carpometacarpus

Plate 3, fig. 3

Material available—Thirty-six specimens.

Characters—Process of metacarpal I with only a slight proximal slant as in *Geranoaëtus* and to a lesser extent *Heterospizias; Urubitinga* varies, and *Buteo* has pronounced proximal slant. Distal end of metacarpal II rounding to join symphysis as in *Buteo borealis; Geranoaëtus* and *Urubitinga* more angular.

Size—Maximum specimen, L.A.M. No. C4448, length 93.0 mm., greatest depth proximal end 22.6 mm., least depth proximal end 19.8 mm., height of M I 12.3 mm. Same measurements for minimum specimen, L.A.M. No. E4592, 81.1 mm., 20.5 mm., 18.2 mm., 12.0 mm. respectively. Mean of length, 87.0 mm.

Pelvis

Plate 5, figs. 1–1b

Material available—Three nearly complete; one with only one side of pelvis complete; one left, one right fragment of pelvis.

Characters—Posterior iliac crest not flaring as broadly as in *Geranoaëtus* and *Buteo* and with notch above acetabulum broad and shallow; resembling in these characters both species of *Urubitinga; Geranoaëtus* and *Buteo* broadly flaring and with distinct notch above acetabulum; *Heterospizias* flaring less widely than *Buteo* or *Geranoaëtus*, and notched more deeply than *Urubitinga*.

Some importance is attached to the character of the posterior iliac crest, primarily because of its constancy within the genus *Urubitinga*, and secondly because of its value in distinguishing between *Geranoaëtus*, *Urubitinga* and *Heterospizias*.

Femur

Plate 5, figs. 2–2b

Material available—Twenty-five complete; two with proximal end broken; two proximal half; three distal half.

Characters—Slender bone with straight shaft and narrow distal end. Trochanter projecting proximally beyond iliac facet somewhat as in *Geranoaëtus*, though slightly

higher, being closer in this respect to *Buteo regalis*. Tendency toward two foramina on anterior side of proximal end, along trochanteric ridge, as in *Geranoaëtus* and *Buteo*.

Size—Greatest length, 107.5 mm. to 95.4 mm.; average 101.0 mm. See table for other measurements.

The femur of *Urubitinga fragilis* is distinguished from that figured as *U. enecta* by Wetmore (1926, p. 3, figs. 1–3) by a straight or externally bowed median intermuscular line on the anterior side and the presence of a second pneumatic foramen proximal to the one noted in the figure of *U. enecta*. In Wetmore's species the intermuscular line bows toward the internal side of the bone, around the single pneumatic foramen. The range in size of *U. fragilis* includes the measurement given for *U. enecta* (breadth through head, 19.5 mm.).

Measurements of Femur

Specimen	a Greatest length	b Breadth proximal end	c Breadth across condyles	d Depth int. cond.	e Depth ext. cond.	Ratio b to a	Ratio c to a	Ratio d to c	Ratio e to c
	mm.	*mm.*	*mm.*	*mm.*	*mm.*	*p. ct.*	*p. ct.*	*p. ct.*	*p. ct.*
Heterospizias U.S.N.M. No. 227378.	77.5	15.8	12.5	11.6	14.4	20.3	16.1	92.9	115.1
Geranoaëtus U.S.N.M. No. 18471..	102.9	21.9	16.8	17.0	19.0	21.2	16.3	101.1	106.7
L. H. Miller No. 233....	111.9	22.4	18.4	18.9	20.3	20.0	16.4	102.8	110.2
Buteo borealis L. H. Miller No. 222....	83.5	17.7	13.9	14.9	16.1	21.1	16.6	107.1	115.8
240....	88.9	17.6	14.2	14.5	15.1	19.7	15.9	102.0	106.1
Buteo regalis L. H. Miller No. 14.....	96.8	19.8	15.8	16.9	18.3	20.4	16.1	107.0	115.8
Urubitinga anthracina D. R. Dickey No. 16950..	71.8	14.5	11.9	12.3	13.5	20.1	16.6	111.4	113.2
15618..	74.9	14.3	12.0	12.2	13.3	19.1	16.0	101.6	103.2
Urubitinga urubitinga L. H. Miller No. 738....	88.5	16.4	13.1	12.5	15.0	18.5	14.8	95.4	114.2
Urubitinga fragilis L.A.M. No. C5857..	97.6	18.1	14.7	14.5	16.3	18.5	15.0	98.6	110.8
D3433..	103.6	20.2	17.0	16.1	18.7	19.5	16.4	94.7	109.9

Tibiotarsus

Plate 6, figs. 2–2c

Material available—Thirteen complete (one with fibula attached); three with broken proximal end; thirteen proximal half; fifteen distal half.

Characters—Buteonine in the broad, shallow intercondylar groove. Proximal end differing from *Heterospizias* in greater development of cnemial crests. Closely resembling *Geranoaëtus*, though relatively more slender (see table).

On the specimens which are unworn, the posterodistal part of the margin of the internal condyle comes to a distinct point (see Plate 6, fig. 2c).

Measurements of Tibiotarsus

Specimen	a Length to proximal articular surface	b Breadth proximal end	c Depth proximal end	d Breadth distal end	e Depth external condyle	f Depth internal condyle	Ratio of b to a	Ratio of c to a	Ratio of d to a	Ratio of e to d	Ratio of f to d	Ratio of b to c
	mm.	*mm.*	*mm.*	*mm.*	*mm.*	*mm.*	*p. ct.*	*p. ct.*	*p. ct.*	*p. ct.*	*p. ct.*	*p. ct.*
Heterospizias												
U. S. Nat. Mus.												
No. 227378.....	120.2	12.4	15.3	13.3	9.5	9.2	12.7	10.3	11.5	71.4	69.2	8.1
Geranoaëtus												
U. S. Nat. Mus.												
No. 18471.....	137.1	16.4	20.8	18.2	11.7	11.4	11.9	15.1	13.2	64.3	62.6	7.8
L. H. Miller												
No. 233.....	152.9	18.5	23.2	20.3	13.7	12.8	12.0	15.1	13.2	67.4	63.0	7.9
U. urubitinga												
L. H. Miller												
No. 738.....	144.2	13.7	15.8	13.8	9.3	9.9	9.4	10.9	9.5	67.3	71.5	8.6
U. anthracina												
D. R. Dickey												
No. 16950.....	104.1	11.1*a*	14.6	12.6	9.2	8.8	10.6	14.0	12.1	73.0	69.7	7.6
15618.....	108.0	11.2*a*	14.7	13.0	9.3	9.0	10.3	18.6	12.0	71.5	69.1	7.6
U. fragilis												
L. A. Mus.												
No. E1138.....	131.7	15.2	18.4	15.5	10.5	10.4	11.5	13.9	11.7	67.7	67.1	8.2
D4847.....	139.9	17.2	20.7	17.7	12.6	11.8	12.3	14.7	12.6	71.2	66.6	8.3
D1677.....	142.3	17.4	21.4	17.8	12.3*a*	12.1*a*	12.2	15.0	12.5	69.1	68.0	8.1
C3731.....	149.6	.....	.....	17.6	12.5	12.4	....	....	11.7	71.0	70.5	....

a, approximate.

Size—Length from condyles to proximal articular surface: 149.6 mm. to 130.4 mm.; average 138.8 mm.

As compared with the figures of *Urubitinga enecta* Wetmore (1923, p. 501, figs. 14–16) from the Miocene of Nebraska, the largest specimen of *fragilis* is about 14 mm. shorter than *U. enecta*. It is further distinguished from the Miocene species in the lesser extent of the condylar surface proximally on the posterior side, and less prominent internal condyle.

TARSOMETATARSUS

Plate 6, figs. 1–1b

Material available—Seventy-five complete; ten incomplete; twenty-one proximal end; twenty distal end.

Characters—Relatively long and slender bone with tubercle for tibialis anticus placed high on shaft. Distinguished from *Geranoaëtus* by (1) slenderness, (2) tubercle for tibialis anticus placed higher on shaft, (3) inner calcaneal ridge placed nearer center of shaft, (4) hypotarsal ridges closer together, (5) posteriormost tip of internal calcaneal ridge long and narrow (*Geranoaëtus* short and broad), (6) anterior margin of proximal articular surface unevenly curved (*Geranoaëtus* straight), (7) internal cotyla deeper relative to breadth of proximal end. Characters 1 to 4 above are as given by Miller (1911, p. 315). In (1) degree of slenderness, *fragilis* is closest to *U. anthracina* as determined by relative breadth of proximal and distal ends (see table); in (2) position of tubercle for tibialis anticus, *fragilis* is nearest *U. anthracina* (see table); in (3–4) position of calcaneal ridges, the similarity lies with *Heterospizias* and *Urubitinga;* in (5) character of posterior tip of internal calcaneal ridge, it is again similar to *Heterospizias* and *Urubitinga;* in (6–7) character of anterior margin of proximal margin of anterior articular surface and depth of internal cotyla, *fragilis* is similar to *Urubitinga*. In the position of the internal proximal foramen at the distal end of the internal

Measurements of Tarsometatarsus

Specimen	a Length	b Breadth proximal end	c Breadth distal end	d Length to middle of tubercle tibialis anticus	Ratio of b to a	Ratio of c to a	Ratio of d to a
	mm.	*mm.*	*mm.*	*mm.*	*p. ct.*	*p. ct.*	*p. ct.*
Heterospizias							
U.S.N.M.							
No. 227378	104.2	13.5	15.3	14.1	12.9	14.6	13.5
Geranoaëtus							
U.S.N.M.							
No. 18471	105.0	18.7	20.0	20.7	17.8	19.0	20.3
L. H. Miller							
No. 233	114.7	20.7	22.8	22.3	18.6	19.9	19.4
U. urubitinga							
D. R. Dickey							
No. 17185	115.3	15.0	16.0	15.0	13.0	13.8	13.0
L. H. Miller							
No. 738	119.5	14.7	16.0	15.7	12.3	13.3	13.1
U. anthracina							
D. R. Dickey							
No. 16950	83.3	13.4	14.1	14.2	16.1	16.9	17.0
15618	88.3	13.5	15.1	14.8	15.3	17.1	16.7
U. fragilis							
L.A.M.							
No. D783	99.0	16.9	19.8	18.8	17.0	20.0	18.1
J9864	103.9	16.1	17.9	14.8	15.5	17.2	14.2

calcaneal ridge, *fragilis* is unlike *Heterospizias* in which the foramen is on the internal side of the ridge.

Size—Length, from 113.4 mm. to 96.3 mm.; average 105.4 mm.

Summary

Fragilis was a species of long-legged eagle of small size and slender build. Though in approximate size and in length of leg it was similar to small *Geranoaëtus melanoleucus*, its general appearance differed from that species in several important respects, namely: (1) a more slender body and limbs; (2) a weaker beak; and (3) longer wings.

The slenderness of *fragilis* is reflected in all of the limb bones as well as the pelvis and sternum; the skull, too, is relatively long and narrow, with a long, slender rostrum, quite unlike the broad, short and sharply curved type of beak characteristic of *Geranoaëtus* and *Buteo*. In these particulars *fragilis* is more closely allied to *Urubitinga* and *Heterospizias;* the wings appear to be relatively longer even than in *Urubitinga*, corresponding more closely to *Heterospizias*.

The differences between *fragilis* and *Geranoaëtus*, shown in the general characters, are further emphasized by the detailed characters of the separate elements, as reviewed in the preceding pages. The facts revealed by this detailed study indicate a closer relationship with *Urubitinga* than with *Heterospizias;* this is brought out particularly in the features of the rostrum and pelvis, as well as in certain details of the tarsometatarsus.

In view of the points set forth above, the writer believes that *fragilis* should be removed from the genus *Geranoaëtus*, and suggests that it be known henceforth as *Urubitinga fragilis* (Miller).

The assignment of *fragilis* to the genus *Urubitinga* constitutes the second fossil record of this genus in the United States. *Urubitinga enecta* Wetmore from the Miocene of Nebraska was apparently a bird of about the same size as *fragilis* though with considerably longer legs. It is worthy of note in regard to the proportions of these two fossil species (in so far as we may judge by the specimens available), that neither agrees with the long-legged *U. urubitinga*, living today, in its greater length of tibiotarsus than of humerus. In both *U. enecta* and *U. fragilis* the humerus is longer than the tibiotarsus,[1] being closer in this respect to *U. anthracina*.

Still another fossil record of the genus *Urubitinga* may be found in two specimens (a coracoid and humerus) from Hawver Cave (see Plate 2, figs. 3–3a, and Plate 3, fig. 2). These specimens were listed as *Geranoaëtus* sp. by Miller (1911b, p. 392); in discussing the specimens, Miller remarked upon the possibility that these bones might later be identified with one of the slender eagles of Rancho La Brea, known at that time from the tarsometatarsus only.

Now that more is known of the skeletons of the eagles of the Rancho La Brea deposits, the Hawver Cave specimens have been borrowed from the University of California Museum of Paleontology for comparisons.

The similarity between the cave coracoid and that of *U. fragilis* is immediately apparent (in Plate 2 compare figures 3 and 3a with figures 2 and 2a). On first glance the two appear to be identical. The cave specimen is distinguishable from *Geranoaëtus melanoleucus* as compared with *fragilis*, on the same bases that *fragilis* and *G. mela-*

[1] This assertion is based upon the assumption that the humerus of *U. enecta*, figured by Wetmore, is from the same individual as the type tibiotarsus with which it was found associated (Wetmore, 1923, pp. 501 and 503, figs. 14–18), and that an approximately correct idea of the proportions of *U. fragilis* may be obtained by a comparison of maximum, minimum, or average specimens of the various elements.

noleucus are separated, *i. e.*, even contour of furcular facet, absence of small pneumatic openings, greater height of proximal end relative to breadth. In the first two characters, both the cave specimen and *fragilis* are closer to *U. anthracina*. That the cave eagle and *fragilis* are not identical, however, is indicated by the greater protrusion of the brachial tuberosity in the former. In none of the fifty-five available specimens of *fragilis* is the arc between the glenoid facet and the brachial tuberosity so wide as in the specimen from Hawver Cave (see ratios of d to a and d to b in following table).

Measurements of Coracoid[1]

Specimen	a Length	b Breadth proximal end	c Height proximal end	d Distance from glenoid facet to brachial tuberosity	Ratio of d to a	Ratio of d to b
	mm.	*mm.*	*mm.*	*mm.*	*p. ct.*	*p. ct.*
U.C. Mus. Pal.						
No. 11050....	57.0	17.5	20.3	10.5	18.4	60.0
Urubitinga fragilis						
L.A.M.						
No. C5931...	51.9	15.6	19.1	8.9	17.1	57.1
H4341...	52.4	17.0	....	9.1	17.3	53.5
D2978...	56.1	17.6	20.7	8.7	15.5	49.5
C398....	57.5	18.1	20.1	9.4	16.3	51.8
Geranoaëtus melanoleucus						
L. H. Miller						
No. 233.....	61.3	19.4	20.9	9.5	15.5	49.0
U. anthracina						
D. R. Dickey						
No. 15618....	41.3	12.0	13.1	7.0	16.8	56.4

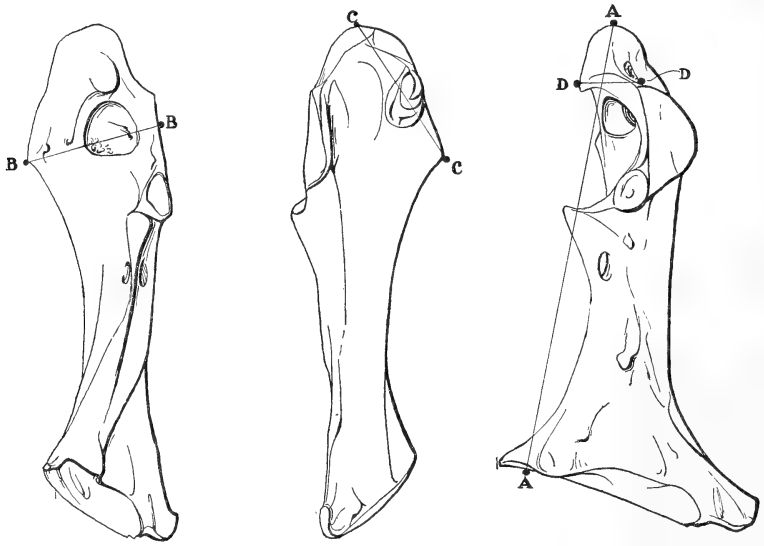

FIG. 2—Drawings of the coracoid of *Urubitinga fragilis* showing positions of the measurements of this element given in the preceding table.

[1] See figure 2 for positions of measurements.

The specimen of humerus (see Plate 3, fig. 2) is a distal end with the greater part of the shaft present. As, in the present writer's opinion, the proximal end of the humerus is more diagnostic than the distal end, this specimen is somewhat difficult to pass judgment upon. However, the curvature of the shaft may be observed, and as the writer has previously noted under the discussion of the humerus of *U. fragilis*, this character appears to be of importance in separating *fragilis* from *Geranoaëtus melanoleucus*. In the cave specimen the curvature is slight as in *U. fragilis*, as distinguished from *G. melanoleucus* in which the curve is more pronounced.

The cave specimen is a generally larger bone than any available representative of either *U. fragilis* or *G. melanoleucus* and surpasses these species also in certain relative measurements, such as breadth and depth of shaft and depth of entepicondyle relative to breadth of distal end (see table of measurements of humerus following). The depth of the shaft relative to its breadth is, however, similar to at least two specimens of *U. fragilis; G. melanoleucus* may possibly attain the same ratio, since the specimen measured overlaps the range of variation in *U. fragilis*, being 0.3 mm. larger than the minimum of the latter. In depth of distal end relative to breadth of same, the cave specimen and *U. fragilis* are close; *G. melanoleucus* is not as deep.

Measurements of Humerus

Specimen	a Breadth distal end	b Depth distal end	c Depth entepi-condyle	d Breadth shaft	e Depth shaft	Ratio of b to a	Ratio of c to a	Ratio of d to a	Ratio of e to a	Ratio of e to d
	mm.	*mm.*	*mm.*	*mm.*	*mm.*	*p. ct.*	*p. ct.*	*p. ct.*	*p. ct.*	*p. ct.*
U.C. Mus. Pal. No. 11015....	29.5	16.4	13.8	18.7	11.1	55.5	46.7	63.4	37.6	59.3
Geranoaëtus melanoleucus L. H. Miller No. 233.....	29.0	15.0	12.6	17.7	9.7	51.6	43.4	61.0	33.4	54.7
Urubitinga fragilis L.A.M. No. C2540...	29.0	15.6	13.4	17.6	10.3	53.8	46.2	60.6	35.5	58.5
C8582...	28.9	15.5	13.0	17.7	9.9	53.6	45.0	61.3	34.2	55.7
D1235...	28.6	15.3	13.0	17.8	9.7	53.5	45.4	62.3	33.9	54.4
D6864...	28.3	16.0	13.1	17.2	10.4	56.5	46.3	60.7	36.7	60.4
D8248...	27.5	15.1	12.8	16.8	9.8	54.9	46.5	61.1	35.6	58.3
C2763...	26.3	14.0	12.0	15.3	8.8	53.2	45.6	58.1	33.4	57.5
C4573...	25.8	13.8	11.4	14.9	8.9	53.5	44.2	57.7	34.4	59.5

From the study of the Hawver Cave specimens as set forth in the above discussion, the writer believes that though these bones are in many respects similar to *U. fragilis* —enough certainly to place the two in the same genus—they are not identical specifically. The name *Urubitinga milleri*[1] is therefore proposed for the species from Hawver Cave, the coracoid (Univ. Calif. Mus. Pal. No. 11050) being designated as the type, the humerus (Univ. Calif. Mus. Pal. No. 11015) as cotype.

Morphnus woodwardi Miller

Plates 7 to 12

Morphnus woodwardi Miller, Univ. Calif. Bull. Dept. Geol., **6**, 312–314, figs. 3a, 3b, 1911.

Morphnus woodwardi was described from a tarsometatarsus in the collections of the University of California. It was assigned to the genus *Morphnus* after a comparison

[1] The writer takes pleasure in naming this species in honor of Dr. Loye Miller, to whom she is primarily indebted for having inspired her interest in avian paleontology and of whose valuable guidance and assistance she continues gratefully to avail herself.

with a cast of the tarsometatarsus of *Morphnus guianensis*. Until the present time no other elements of the skeleton have been identified. Now, with all of the more important skeletal parts represented by at least one or two specimens, it is possible to present a more complete picture of this large buteonine eagle.

It is unfortunate that a complete skeleton of *Morphnus guianensis* has not been available for use in this study. Without it, of course, this work is incomplete. In many respects *woodwardi* has been found to resemble *Geranoaëtus*, in still others *Urubitinga*, *Heterospizias* and *Harpyhaliætus*. Possibly, if a comparison could be made with *Morphnus*, the fossil species would be found to resemble that genus as closely, or even more closely than the other genera to which it has been possible to compare it. For this reason, *woodwardi* is maintained under the genus *Morphnus*, in spite of its resemblances to other genera.

Skull and Mandible

Plate 7, figs. 1–3

The cranium, rostrum and mandible are dissociated and can not with certainty be assigned to *Morphnus woodwardi*. They are grouped together and placed in this species, however, on the basis of their large size and general resemblance to the Buteoninæ.

cranium

Material available—Three specimens.

Characters—In general shape similar to *Geranoaëtus melanoleucus;* broadly rounded dorsally; posterior bulge of supraoccipital broad and less prominent than *Urubitinga* or *Heterospizias*. Slightly larger than *Geranoaëtus*, and with differences in the region of the sphenoidal rostrum.

rostrum

Material available—Three specimens, in a fragmentary condition.

Characters—Palate narrow as in *fragilis* and *Urubitinga*. External nares very long and narrow. Maxillo-palatines close together, but appearing to have very narrow valley between (due to fragmentary condition of specimens, this character is not clear).

mandible

Material available—One symphysis.

Characters—Symphysis long, narrow and heavy.

Furcula

Plate 7, figs. 4 and 4a

Material available—One left clavicle with symphysis; two left, three right clavicle.

Characters—Broad and relatively flat shafts of clavicles with broad ends. Furcular process well developed posteriorly, though shorter than in *Geranoaëtus*. Ventral edge of symphysis notched at furcular process (best noted from anterior side). Intermuscular line of posterior side close to outer margin of clavicle as in *fragilis*, *Heterospizias* and *Urubitinga*. Outer margin of clavicle thick, with no indication of curving posteriorly as in *Urubitinga* (*Geranoaëtus* and *Buteo* also curve posteriorly, though to a less extent than in *Urubitinga);* nearer *Heterospizias*, but not identical.

Size—Length: 79.2 mm.

Sternum

Plate 8, figs. 1 and 1a

Material available—Two, nearly complete.

Characters—Sternum long, with short carina and long xiphial area. Sterno-coracoidal impression extending to fourth costal process as in *Urubitinga* and *Harpy-*

haliætus, with tendency to curve posterior to the ridge before ending, as in the latter genus; impression extends beyond fourth and usually to fifth in *Buteo, Geranoaëtus, Heterospizias* and *Parabuteo*. Xiphial area long and narrow, and convex; closest to *Urubitinga urubitinga* in length but more convex. Sternal plate markedly convex.

Coracoid

Plate 7, figs. 5–5b

Material available—Twelve specimens.

Characters—Buteonine in possessing no distinct distal margin of the furcular facet. Facet smoothly contoured, and pneumatic foramen poorly developed as in *Harpyhaliætus*. Small pneumatic foramina absent as in *Harpyhaliætus, Heterospizias* and *fragilis*. Head thick as in *Harpyhaliætus;* thicker, as well as relatively shorter and broader than *fragilis*, and more blunt anteriorly. Attachment of coracobrachialis prominent. Scapular facet shallow and roughened.

Size—Height: 73.2 mm. to 67.7 mm.; average 69.5 mm.

Scapula

Plate 8, figs. 2–2b

Material available—Eight specimens.

Characters—Anterior border of acromion not straight as in *Geranoaëtus melanoleucus* and *Heterospizias*, but better developed anterodorsally, though not to the extent found in *fragilis* and *Urubitinga anthracina;* differing from these species also in greater development of ventral portion of acromion. Outer margin of glenoid facet straight as in *Urubitinga anthracina*, and unlike *Geranoaëtus*. Margin of bone from upper part of shaft along inner side of tip of acromion only slightly curved, differing from *Geranoaëtus* and *Buteo*. Depression on ventral side posterior to head. Border of glenoid facet angular at its anterior end with notch between angle and coracoidal articulation; the angle is more prominent than in *fragilis*.

Size—Breadth of anterior end: 28.4 mm. to 24.6 mm.; average 25.8 mm.

Humerus

Plate 9, figs. 1 and 1a

Material available—One complete; one with broken distal end; six proximal half; four distal half.

Characters—Comparatively straight shaft and short deltoid crest as in *Heterospizias* and *Urubitinga urubitinga*. Bicipital crest very long, appearing as a flange projecting beyond the shaft on the anconal side. Shaft excavated at the distal end of the median crest. Pneumatic foramen broad and squared at proximal portion. Brachial depression deeply excavated on internal side, giving rise to a distinct ridge running proximally from the attachment of the anterior articular ligament. Deltoid crest prominent and standing away from shaft at its distal end. Margin of deltoid crest about as in *Geranoaëtus*—less irregular than *Urubitinga urubitinga* and more than *Heterospizias*.

Size—Measurements of one complete specimen, L.A.M. No. C6743: Length, 201.7 mm.; breadth of proximal end, 36.9 mm.; breadth of distal end, 34.2 mm.; length of deltoid crest, 72.9 mm. Estimated extremes of length based on broken specimens: 217.5 mm. to 193.1 mm.

Ulna

Plate 10, figs. 1–3b

Material available—Four proximal, four distal half. Though no complete ulna of this species has been found, these specimens are taken to be proximal and distal ends of ulnæ of the same species because of their size, general characters and relative abundance.

Characters—Short external condyle. Olecranon moderately high as in *Geranoaëtus* and *fragilis*, but a little more pointed than in these species. Surface between olecranon and external cotyla faintly depressed; between *Geranoaëtus* and *Heterospizias* in this character (*Gerancaëtus* less faintly depressed, *Heterospizias* more so).

Radius

Plate 9, fig. 2

Material available—Five proximal half. No complete radius is available and the distal ends in the collection are not sufficiently diagnostic to assure correct identification.

Characters—Ligamental papilla elongated as in *Geranoaëtus;* heavier than in *Urubitinga*, less heavy than in *Heterospizias.*

Carpometacarpus

Plate 9, fig. 3

Material available—Eleven specimens.

Characters—Long and slender with relatively short head. Process of metacarpal I slanting proximally as in *Buteo* and some individuals of Urubitinga. Distal end of M III joining symphysis at an angle as in *Geranoaëtus.* Tendinal groove external distally, but curving decidedly so that its proximal extremity is clearly visible on the anterior face of the bone.

Size—Length: 128.4 mm. to 104.4 mm.; average 116.3 mm.

Measurements of Carpometacarpus

Specimen	Length	Greatest depth proximal end	Least depth proximal end	Height, process metacarpal I
	mm.	*mm.*	*mm.*	*mm.*
L.A.M. No. C5187.....	128.4	29.4	26.0	17.3
D2238.....	104.4	24.6	21.3	14.4

Pelvis

Plate 11, figs. 1 and 1a

Material available—One posterior portion of sacrum and left side of pelvis; three fragments of posterior portion of pelvis, without sacrum.

Characters—The posterior iliac crest is broken so that the degree of flaring can not be ascertained. A shallow, pit-like depression is present on the dorsal roof of the ilium above the acetabulum. Center of dorsal side of sacrum indented as a narrow trough. Ilio-ischiatic fenestra egg-shaped and relatively (as well as actually) higher than in *fragilis.* On the basis of these fragmentary specimens, generic comparisons are impossible.

Femur

Plate 12, figs. 1–1b

Material available—Three complete; four distal end.

Characters—Straight shaft; trochanter inconspicuous, but projecting proximally above the iliac facet as in *Heterospizias* and to a less extent *Geranoaëtus* and *Buteo.* Two pneumatic foramina.

Size—Length of complete specimens: 130.7 mm. to 124.6 mm.; distal ends present indicate still larger individuals.

Measurements of Femur[1]

Specimen	Length	Breadth proximal end	Breadth across condyles	Depth int. condyle	Depth ext. condyle
	mm.	*mm.*	*mm.*	*mm.*	*mm.*
L.A.M.					
No. C1111.....	130.7	26.8	21.5	20.5	24.0
D2487.....	124.6	25.3	21.7	19.6	22.9

TIBIOTARSUS

Plate 11, figs. 2–2b

Material available—Five specimens nearly complete; one with proximal end broken; one proximal end; five distal end.

Characters—Broad, shallow intercondylar groove. Inner cnemial crest short, and of a prominence similar to *Buteo* and *Geranoaëtus*. Ligamental tuberosity on internal side of distal end well anterior in position as in *Urubitinga; Heterospizias, Geranoaëtus, Buteo* and *fragilis* more nearly central. Supratendinal bridge long and noticeably broader at its proximal than at its distal end—closest to *Geranoaëtus*, though differing therefrom in the presence of a slight depression between the shaft and the proximal end of the bridge.

Size—Length from distal extremity to proximal articular surface: 190.8 mm. to 171.4 mm.; average 177.7 mm. Ratios of breadth of proximal and distal ends relative to length: average 12.5 per cent and 12.7 per cent respectively.

TARSOMETATARSUS

Plate 12, figs. 2 and 2b

Material available—Thirty complete, three proximal, three distal half.

Characters—Miller gives the characters of the type specimen of *M. woodwardi* as follows (1911a, p. 312): "Resembling *Aquila* in general but 30 per cent longer; shaft narrower, ligamentous bridge shorter; anterior proximal depression shallower and less defined; papilla of tibialis anticus placed much higher on the shaft; ridges of the hypotarsus less produced; foot narrower and trochleæ smaller." In presenting his reasons for assigning *woodwardi* to the genus *Morphnus*, he compares the characters of *Morphnus* and *Geranoaëtus*, as follows (*op. cit.* pp. 312–313): "The differences between *Morphnus* and *Geranoaëtus* as displayed by the tarsometatarsus are slight, and are limited so far as is noticeable to the head region of the bone. In *Geranoaëtus* the anterior face in this region resembles *Haliaëtus* in the great length of the supratendinal bridge. The crest marking its external end falls almost in the center of the bone as in *Haliaëtus*. This face of the bone is also less abruptly excavated—a character distinguishing *Haliaëtus*. A further distinguishing character appears when the proximal articular surface is viewed. The inner hypotarsal ridge shows much the greater development in *Geranoaëtus*."

The following characters have been found to remain constant throughout the series of tarsometatarsi now available:

Similar to *Geranoaëtus* in general shape and proportions, but with the following differences: (1) internal calcaneal ridge relatively more slender and with correspondingly smaller posterior end of ridge; this end is broad, however, as in *Geranoaëtus*, not narrowly oval as in *fragilis;* (2) number of proximal foramina present on posterior side varying from two to four, the majority of specimens having three; there may be two external, situated one above the other, and two internal with the proximal one

[1] See Measurements of Femur under *Urubitinga fragilis* to compare with *U. fragilis* and modern species.

distal to the calcaneal ridge, or slightly internal to the distal end of the ridge, the other distal to the first; unfortunately in the cast of *Morphnus guianensis* at hand, the foramina are not represented; (3) internal border of internal cotyla deeper anteroposteriorly; closer to *M. guianensis;* (4) external calcaneal ridge not distinctly marked off from articular surface; closer to *M. guianensis;* (5) distal end flatter transversely; nearer *M. guianensis.* Distinguished from *M. guianensis* in (a) greater length; (b) proportions: shaft narrow in center, flaring to broad ends; anteroposterior depth of shaft as in *Geranoaëtus; M. guianensis* of approximately same breadth throughout length of bone, and with very great depth of shaft anteroposteriorly (see ratio of e to c in table).

Size—Length: 140.6 mm. to 125.0 mm.; average 131.5 mm.

Measurements of Tarsometatarsus

Specimen	a Length	b Breadth proximal end	c Breadth distal end	d Distance to middle of tub. for tibialis anticus	e Depth shaft	Ratio c to a	Ratio d to a	Ratio e to c
	mm.	*mm.*	*mm.*	*mm.*	*mm.*	*p. ct.*	*p. ct.*	*p. ct.*
Geranoaëtus L. H. Miller No. 233.....	114.7	20.7	22.8	22.3	9.5	19.8	19.4	41.6
U.S.N.M. No. 18471...	105.0	18.7	20.0	20.7	8.9	19.0	19.6	44.5
Morphnus guianensis L. H. Miller collection .	103.8	16.3	18.5	18.0	10.3	17.8	17.3	55.6
Morphnus woodwardi L.A.M. No. D4679..	136.7	24.5	27.9	23.9	12.2	20.4	17.4	43.7
D3169..	134.6	24.8	28.4	24.7	12.6	21.0	18.3	44.3
D3168..	131.9	21.7	25.6	20.0	10.6	19.4	15.1	41.4
D4486..	129.4	22.4	26.3	23.9	12.1	20.3	18.4	46.0
D1971..	127.1	22.4	24.3	21.0	10.9	19.1	16.5	44.8

SUMMARY

Morphnus woodwardi, like *Urubitinga fragilis* was a species of long-legged eagle, the proportions of the two being about the same. *Woodwardi,* however, was a larger and heavier bird, more closely approximating *Aquila chrysaëtos* in body size, though averaging larger even than that species; *woodwardi* can not be likened to *Aquila,* however, since in proportions and all characters of individual elements it is decidedly buteonine.

In detailed characters of the separate elements, *woodwardi* shows similarities with *Urubitinga, Heterospizias, Harpyhaliætus, Geranoaëtus* and *Buteo,* as well as with *Morphnus* in the tarsometatarsus. The specimens available, however, do not show consistent similarity with any one of these genera. For this reason, in spite of the fact that we are unable to compare the entire skeleton of *woodwardi* with that of *Morphnus,* the species is maintained in the latter genus.

SUBFAMILY AQUILINÆ

The discussions of *Aquila chrysaëtos, Spizaëtus grinnelli,* and *Haliæëtus leucocephalus* are included under the subfamily Aquilinæ. Though in the osteological characters under discussion, the present

writer does not consider that *Haliœëtus* is a typical member of this subfamily, it is more appropriately placed here than with the Buteoninæ.

Aquila chrysaëtos (Linnæus)

Specimens of *Aquila* in the Los Angeles Museum collections from Rancho La Brea are twice as abundant as those of the other eight species under consideration combined. A good series of each element is available, the tarsometatarsus being most numerous, with over 1900 specimens. The total of all specimens is approximately 9500.

In the present study of *Aquila* from Rancho La Brea, the writer's observations are in agreement with those of Miller (1911a, pp. 307–308 and 1925b, pp. 95–96) regarding specific identity with *Aquila chrysaëtos*. Miller (1925b, p. 96) has commented on the great range of variation in the fossil representative of this species in the matter of size, though with perfect intergradation from the largest to the smallest individuals. The question is raised as to whether or not this variation exceeds that of modern *A. chrysaëtos*.

Though the series of skeletons of the modern form now available is small and does not have as great a range of variability as the fossil, there are present in this series specimens which equal and even fall below the minimum of the fossil in certain elements, though there are none which equal the maximum. A comparison of the size variations of the fossil and the modern forms as indicated by the limb bones and coracoid is illustrated in the table of "Comparative Measurements and Proportions of the Rancho La Brea Eagles and Related Modern Forms" on page 78. In this table the largest and the smallest specimens of each element are listed for the Rancho La Brea form. For the modern, the largest and smallest specimens are given, but since these skeletons are incomplete, two others, which are complete, are presented, one next to the maximum in size, the other next to the minimum.

In the humerus and ulna, the minimum in the fossil does not fall as low as the minimum of the Recent, in spite of the tremendous range in size of the former. It is, of course, possible that could the entire series of fossil humeri and ulnæ be measured, specimens as small as the Recent would appear; since these two elements are long and comparatively slender, and therefore fairly fragile, they are represented in the fossil *Aquila*, by only a small proportion of complete bones capable of being measured (about 15 per cent of the total number of each, or 142 complete humeri and 71 complete ulnæ). Should smaller bones be present, they would, of course, increase the range in size of the fossil form; as it is, the maximum of the fossil exceeds the maximum of the Recent by 22.0 mm. in the humerus and 17.1 mm. in the ulna. The greater length of these elements is reflected also in the ratios of maximum and minimum length of leg to maximum and minimum length of wing respectively. There is a difference of approximately 4 per cent between these ratios in the fossil and in the modern forms. Too much weight should not be placed on these facts, however, in view of the impossibility of accurate comparison of the fossil with the Recent bird; the series of modern specimens is inadequate, and in spite of the good series of fossil specimens, actual individuals can not be recorded. Therefore, these ratios can be considered only in a general way. For these reasons, though the table would seem to indicate that the fossil *Aquila* had relatively longer wings than the existing Golden Eagle, the writer does not consider the evidence to be of sufficient accuracy to warrant basing definite conclusions thereon.

The Rancho La Brea species has been compared also with those described by Shufeldt from the Pleistocene of Oregon. Since, however, Shufeldt's species are based

on different physical characters of the elements from which they are described, while the Rancho La Brea form varies from the modern only in the matter of size, if it varies at all, the possibility of identifying the Rancho La Brea bird with either *A. sodalis* or *A. pliogryps* is discarded.

Furthermore, it is not improbable that could these species be studied with a greater variety of genera for comparison than was available to Shufeldt at the time of description, *pliogryps* and *sodalis* might be removed from the genus *Aquila*. Referring to the position of the internal proximal foramen in the tarsometatarsus of *sodalis*, Shufeldt (1892, p. 417) remarks on the inadequacy of his series for determining the constancy of this character. It is the present writer's experience that the position of this foramen with respect to the hypotarsus varies but slightly within a species, or within a genus. The position of the foramen in *sodalis*, as described by Shufeldt is "just at the lower point of commencement of the inner and larger process of the hypo-tarsus. In this last character it agrees with a specimen of *H. leucocephalus* at my hand." Judging from this "word picture" the position does not agree with either *Aquila* or *Spizaëtus* (which resembles *Aquila* in many respects). In these genera the foramen is located on the internal side of the larger process of the hypotarsus near its distal commencement, and it in no way approximates the position in *H. leucocephalus*. It is the writer's opinion, therefore, that upon further comparison, *sodalis* may be identified with a genus other than *Aquila*, not necessarily *Haliæëtus*, however, for there are other genera, particularly among the Buteoninæ, in which the foramen occupies a position similar to the one described for *sodalis*. It would be necessary to study the specimen itself, considering other points relating to the character of the bone in that region.

A. pliogryps, described merely from phalanx 1 of the hallux, (Shufeldt, 1892, pp. 416–417, and fig. 33, pl. 17) seems scarcely deserving of species designation, and may possibly belong with the tarsometatarsus described as *A. sodalis*. As with this latter species, its assignment to *Aquila* is questioned; the slender phalanx seems better suited to a species of the subfamily Buteoninæ.

With regard to the other occurrences of *Aquila* in the fossil record, Wetmore (1923, p. 504) reported one from the Miocene of Nebraska, based on a distal end of left radius which he assigned to the genus *Aquila*, declining to give a specific designation thereof in view of the scant material. Three species were reported by Shufeldt (1913b, pp. 297–298) from the Eocene of Wyoming, all based upon fragmentary material. One, *Aquila antiqua*, Shufeldt later found to be related to the owls; for this species he described a new genus, *Minerva* (1915, p. 43). The type specimen of *antiqua*, an ungual phalanx, he characterized (1913b, p. 297) by the "prolongation of the dorsal arc of the claw over the articulation, which articulatory surface, however, is continued on to this process." *Aquila ferox*, described in the next paragraph is based on a "perfect pedal phalangeal joint, apparently basal joint of the second toe. Also the proximal portion of a claw. . ." This claw, Shufeldt continues, "exhibits to a marked degree the character described above—that is, the prolongation of the dorsal arc over the articulation." There follows a brief description of the "joint," with a concluding statement, "This eagle was about the same size as the last, or perhaps rather smaller." As far as the description goes, therefore, there is no reason, other than a possible size difference for separating the species *ferox* from the species *antiqua*.

Aquila lydekkeri, next described (Shufeldt, 1913b, p. 298), is based upon several phalanges, including two claws, as well as fragments of the tibiotarsus, femur and tarsometatarsus. This bird, Shufeldt says, was a "large species of eagle." The description of the tibiotarsus, however, sounds more strigine than aquiline—"the

condyles of the tibio-tarsus are thick, parallel to each other, and the valley between them narrow and deep antero-posteriorly." Added to this, one of the claws is described as possessing the prolongation of the dorsal arc characteristic of *antiqua*. Possibly, then, *lydekkeri* is also synonymous with *antiqua*, although there is a slight discrepancy in size—*antiqua* is estimated to be about the size of *Pandion*, the tibiotarsus of *lydekkeri* is given as 16 mm., which is about 1.5 mm. greater than the specimen of *Pandion* at hand, which, however, might be accounted for by individual variation. Why Shufeldt characterized *lydekkeri* as a "large species of eagle" is difficult to understand, since the measurement given for the distal end of the tibiotarsus falls 3 mm. below the smallest available specimen of *A. chrysaëtos* from the asphalt. Taking all of the above points into consideration, the present writer believes that *ferox* and *lydekkeri* belong with *antiqua* in the genus *Minerva*, and possibly represent individual variations of the species *antiqua*. It should be noted here that Wetmore, in compiling the list of fossil birds of North America for the fourth edition of the American Ornithologists' Union Checklist (1931), questioned the propriety of the generic allocation of *ferox* and *lydekkeri*.

Spizaëtus grinnelli (Miller)

Plates 14 to 19

Geranoaëtus grinnelli Miller, Univ. Calif. Publ. Geol., **6**, 314–315, figs. 4a-4b, 1911.

This species was described from a tarsometatarsus in the collections of the University of California at Berkeley. On the basis of the characters of the tarsus, *grinnelli* was placed in the genus *Geranoaëtus*, comparisons having been made with *G. melanoleucus*. At this time, no other elements of the skeleton of *grinnelli* had been identified.

Nearly the entire skeleton of this species is now available. With this addition to the knowledge of *grinnelli*, it has been possible to make a more thorough study of its relationships. Recently, through the courtesy of Mr. Donald R. Dickey, it has been the present writer's privilege to examine two partial skeletons of *Spizaëtus ornatus* from Salvador. As a result of this examination and of a comparison with *grinnelli*, the writer is convinced that the relationship of the latter is closer to *Spizaëtus* than to any other genus heretofore examined. In general characters there is little distinction between *S. ornatus* and *grinnelli* except in size, *S. ornatus* being smaller than *grinnelli*. There is another species of *Spizaëtus* (*S. tyrannus*) living in Central and South America, but judging from the measurements of tarsus as given in the Catalogue of Birds of the British Museum (Sharpe, 1874, p. 264), this species, also, is smaller than *grinnelli*. The genus is present in Africa, India, Indo-Malaya, Celebes, Formosa and Japan, but though some of the species represented are larger than those of South America, in all but one, the measurements of male tarsus fall below the minimum of *grinnelli*. In the one excepted species, *S. bellicosus* from South Africa, the female tarsus is given as 5.2 inches (Sharpe, 1874, p. 266), or about 130 mm.; this is 16 mm. greater than the maximum for *grinnelli*. It is scarcely possible, therefore, that the Pleistocene species is identical with any species now living. In view of the facts set forth above, the writer feels justified in suggesting that *Geranoaëtus grinnelli* Miller be known hereafter as *Spizaëtus grinnelli* (Miller).

A detailed description of the separate elements follows.

Skull and Mandible

Plate 14, figs. 1–3

The cranium, rostrum and mandible are separate from each other in the collection, and there is no conclusive proof that they belong to *grinnelli*, or even all to the same

species. However, as we have previously stated (on page 13), evidence favors the placing of these specimens with *grinnelli* for the reason that the only other specimens which could possibly be attributed to this species have characters close to *Buteo* and *Urubitinga*, and thus agree better with *Urubitinga fragilis*, while these under consideration show the greater resemblance to *Aquila* which is noticeable in the tarsometatarsus and other elements assigned to *grinnelli*. Unfortunately, no specimens of the skull and mandible of *Spizaëtus* are available for comparison.

Cranium—The nine specimens of cranium are somewhat fragmentary and it would be difficult to present a description here which would prove of value in identification. In general it may be said that the cranium resembles a small *Aquila*. The reader is referred, also, to the illustrations, Plate 14, figures 1, 1a and 1b.

Rostrum—Three specimens available, all very fragmentary. These specimens show characters similar to *Aquila*, except for the presence of a median ridge in the anterior portion of the premaxillary region on the ventral side, and the absence of a flange-like protuberance at the anterior end of the external naris. (See Plate 14, figs. 2 and 2a.)

Mandible—Specimens available: one complete, two fragments of articular portion. As with the cranium, the most that can be said of the mandible is that it is generally similar to *Aquila*, though possessing certain distinguishing characters difficult to describe. (See Plate 14, fig. 3.)

Sternum

Plate 15, figs. 1 and 1a

Material available—Twelve specimens, two of which are nearly complete.

Description—Similar to *Aquila* and *Spizaëtus*—posterior border of sterno-coracoidal impression tending to curve posterior to fourth costal process, then curving anteriorly again to end at, or slightly posterior to this process; border of impression rounded; this character distinguishes *grinnelli* from the Buteoninæ, in which subfamily the posterior border of the sterno-coracoidal impression is straight and proceeds directly from the coracoidal sulcus to the fourth or fifth costal process, where it ends.

Similar to *Spizaëtus*, and to a lesser extent to *Geranoaëtus*—intermuscular line from ventral lip of coracoidal sulcus forming an obtuse angle with ventral lip of sulcus and running nearly parallel to ventral border of sterno-coracoidal impression; this line forming a right angle with ventral lip of coracoidal sulcus in *Aquila*.

Similar to *Spizaëtus*—xiphial area distinctly marked off from sternal plate by raised borders; tendency to presence of pneumatic openings at anterior end of sterno-coracoidal impression (these pneumatic openings are not present in all individuals either of *Spizaëtus ornatus* or of *grinnelli*, but do occur in some, whereas none have been noted in any available specimen of any other species).

Distinct from *Spizaëtus ornatus*—xiphial area broader; anterior carinal margin straighter (noticeably curved in *S. ornatus*).

Furcula

Plate 14, figs. 4 and 4a

Material available—One complete; four left clavicle with symphysis; five left clavicle; seven right clavicle; one symphysis.

Description—Similar to *Spizaëtus*: narrower (more oval) than *Buteo* or *Aquila*, and even slightly narrower than *Geranoaëtus*; furcular process and symphysis extended posteroventrally, and process not prominent at dorsal margin; process equally developed at both dorsal and ventral margins in *Geranoaëtus* and extending posteriorly; process not prominent at dorsal margin in *Aquila* and extending ventrally below symphysis; symphysis not extended in either *Aquila* or *Geranoaëtus*. Dorsal ends of clavicles irregular in outline and narrow with rounded tips (*Geranoaëtus* evenly outlined, and *Aquila* with tips tapering to a point).

Distinguished from *Spizaëtus ornatus*: anterior aspect of symphysis evenly triangular in shape without depression at ventral edge.

Size—Length: 59.6 mm. to 58.3 mm. in *grinnelli*; 44.4 mm. in *S. ornatus*.

Coracoid

Plate 15, figs. 2–2c

Material available—Fifty specimens, practically complete.

Description—Similar to *Aquila* and *Spizaëtus* as distinguished from the Buteoninæ, by the presence of a distinct posterior margin on the furcular facet.

Similar to *Spizaëtus*, and distinguished from *Aquila* by (1) the character of the furcular facet, the internal border of which is not rounded as in *Aquila*, but has a "chopped off" appearance (see Plate 15, figs. 2 and 2b); (2) head broad from left to right (see Plate 15, fig. 2c).

Size—Length: *grinnelli*, 63.3 mm. to 52.3 mm.; *ornatus*, 48.6 mm.

Measurements of Coracoid

Specimen	a Length	b Distance from sternal facet to procoracoid	c Breadth furcular facet	Ratio of b to a	Ratio of c to a
	mm.	*mm.*	*mm.*	*p. ct.*	*p. ct.*
Spizaëtus grinnelli L.A.M.					
No. H4412.....	52.3	34.0	16.1	65.1	30.8
E4671.....	54.6	34.7	17.9	63.6	32.7
H4369.....	55.3	36.5	17.0	66.1	30.7
C5278.....	56.7	35.5	19.4	62.6	34.2
C2052.....	60.8	39.5	19.4	65.0	31.9

Scapula

Plate 15, figs. 3–3b

Material available—Thirty-nine specimens.

Description—Similar to *Aquila* and *Spizaëtus*: (1) acromion extended anteriorly and dorsally with anterior margin evenly rounded and sloping from ventral to dorsal sides; differing from *Geranoaëtus* and *Buteo*, in which the acromion protrudes at the anteroventral edge as well as dorsally, thus presenting an angular aspect; (2) internal face of acromion with only faint depression; *Geranoaëtus* with marked depression; *Spizaëtus* with depression faint to absent; *Aquila* with depression absent.

Glenoid facet irregularly convex, with ridge at distal margin; unlike *Geranoaëtus* and *Aquila*; this portion can not be seen on the partially articulated skeletons of *Spizaëtus* available for comparison.

Size—Breadth of proximal end, 23.8 mm. to 17.7 mm.

Humerus

Plate 16, figs. 1 and 1a

Material available—Fourteen complete, nineteen proximal half, twelve distal half.

Description—Not identical with any other species available, though closest to *Spizaëtus*. It should be noted here that characters of the humerus may vary in the different species of a genus, *e. g. Urubitinga urubitinga* and *U. anthracina*.

(1) A heavy bone with (2) shaft greatly curved; (3) entepicondylar prominence well inflated; (4) deltoid crest pointed at distal extreme, but with curved margins immedi-

ately proximal to tip; (5) bicipital crest rounded and having (6) rounded, but distinct distal margin;[1] (7) pneumatic fossa broadly rounded and (8) heavily bordered.

The above characters which can be compared with modern species are as follows: (2) *Spizaëtus*; (3) *Aquila* and *Spizaëtus*; (5) *Spizaëtus* and one specimen of *Geranoaëtus*; (6) one specimen of *Geranoaëtus*; (7) near *Spizaëtus*.

Size—See table.

Measurements of Humerus

Specimen	Length	Breadth dist. end	Breadth prox. end	Length deltoid crest	Length bicipital crest
	mm.	*mm.*	*mm.*	*mm.*	*mm.*
Spizaëtus grinnelli					
L.A.M.					
No. D2626	142.0	25.3	26.6	53.2	24.3
B8708	146.2	25.7	27.1	55.5	26.2
C4101	147.0	25.7	28.3	56.1	26.4
C2548	149.1	26.7	29.7	55.7	27.3
C297	153.9	26.0*a*	29.7*a*	59.3	27.7
C5741	156.2	27.8	30.2	59.9	28.6
E1070	156.7	28.7	31.5	60.8	28.7
E1069	157.2	28.2	31.5	....	30.0
D4705	157.9	....	31.7	61.2	28.8
C9092	159.6	28.5	....	62.0	....
D2365	159.8	28.6	32.0	61.4	30.0
D4800	169.9	30.5	34.8	66.6	33.0
B9326	172.1	30.9	34.7	66.1	34.2
D3036	173.1	31.0	34.8	66.5	32.6
Spizaëtus ornatus					
D. R. Dickey					
No. 16872	116.0	22.7	23.9	46.6	25.3
Geranoaëtus melanoleucus					
U. S. Nat. Mus.					
No. 18741	145.0	....	28.3	58.4	....
L. H. Miller					
No. 233	160.0	....	32.0	61.8	....

a, approximate.

Ulna

Plate 17, figs. 1–1b

Material available—Six complete; thirteen proximal half; fourteen distal half.

Description—Similar to *Aquila*, as distinguished from *Geranoaëtus*: (1) surface between olecranon and external cotyla very faintly depressed; in *Geranoaëtus* there is a notch or pit in this region; (2) olecranon, as viewed from internal side, more rounded at tip; (3) prominence for anterior articular ligament (at proximal end) larger.

Distinguished from both *Aquila* and *Geranoaëtus*: (1) humero-ulnar depression (at proximal end) deeper; (2) carpal tuberosity (at distal end), as viewed from palmar side, less abruptly marked off from shaft. There are no specimens of this element of *S. ornatus* available.

Size—Length: 200.6 mm. to 165.5 mm.

Radius

Plate 17, figs. 2 and 2a

Material available—Two complete; ten proximal half; distal end not sufficiently diagnostic for identification apart from proximal end.

[1] Possibly a variable character as, of the two specimens of *Geranoaëtus melanoleucus* available one has a rounded distal border, the other angular.

Description—Similar to *Aquila* and distinguished from *Geranoaëtus* by the character of the ligamental papilla at the proximal end (more definitely a papilla in *Aquila* and *grinnelli*, and not slightly elongated as in *Geranoaëtus*). There are no specimens of this element of *S. ornatus* available.

Size—Length: L.A.M. No. J9313, 171.2 mm.; L.A.M. No. E1508, 161.2 mm.

Carpometacarpus

Plate 16, figs. 2 and 2a

Material available—Fifty-four practically complete.

Description—A heavy bone with wide intermetacarpal space and well-curved metacarpal III, thus somewhat resembling *Aquila*. Unfortunately, this element of *Spizaëtus ornatus* is lacking in the skeletons available.

Distinguished from *Aquila* by (1) the character of the distal metacarpal symphysis, which though more nearly similar to *Aquila* than to *Geranoaëtus*, differs from that genus in the nature of the excavation on the internal face, and in its relatively greater height; and (2) the tendinal groove on metacarpal II, which is straighter and more lateral in position throughout its extent.

Size—See table.

Measurements of Carpometacarpus

The 50 specimens of this element which can be measured fall into 17 groups with regard to length, as follows: 72 mm., 1 specimen; 74 mm., 3 specimens; 76 mm., 2 specimens; 78 mm., 3 specimens; 79 mm., 4 specimens; 80 mm., 7 specimens; 81 mm., 7 specimens; 82 mm., 9 specimens; 83 mm., 5 specimens; 84 mm., 2 specimens; and one each for the following: 90 mm., 92 mm., 93 mm., 94 mm., 95 mm., 96 mm., 97 mm. In the measurements given here, one specimen has been taken from each group.

Specimen	Length	Greatest depth proximal end (int. side of trochlea to process of M I)	Least depth proximal end (ext. side of trochlea to process of M I)
	mm.	*mm.*	*mm.*
Spizaëtus grinnelli			
L.A.M.			
No. E1938.....	72.6	19.0	16.5
D4713.....	74.5	19.4	17.0
E994.....	76.6	19.6	17.2
H2620.....	78.9	22.0	19.5
B9809.....	79.7	21.1	18.6
C7980.....	80.3	21.6	19.1
B9729.....	81.6	21.7	19.2
E3769.....	82.9	21.7	18.9
B9903.....	83.6	21.5	19.0
H2616.....	84.0	21.8	19.3
C679.....	90.8	22.8	19.5
C7325.....	92.0	23.8	20.5
C7330.....	93.6	23.3	20.4
C2776.....	94.6	23.8	20.7
H2707.....	95.0	24.3	21.5
B9810.....	96.0	24.4	21.4
D1440.....	97.0	24.6	21.7

Pelvis

Plate 18, figs. 2–2b

Material available—Five, sacrum and pelvis; five fragments of pelvis.

Description—Similar to *Aquila* and *Spizaëtus* in concavity of external margin of ilium posterior to antitrochanter.

Similar to *Spizaëtus*: ischium, and portion of ilium immediately adjacent, short and broad; ilio-ischiatic fenestra definitely margined posteriorly and dorsally; ilium not extending laterally beyond parapophyses of lumbar vertebræ; parapophyses slanting decidedly upward; lumbar region as viewed from above, very narrow, with ilia sloping steeply from the median dorsal ridge with no lateral flare at ventral edge; tendency to pneumaticity of the ilium anterodorsal to the antitrochanter.

Distinguished from *Spizaëtus ornatus*: iliac crests less well developed and not uniting to form median dorsal ridge as far posteriorly as in *Spizaëtus*. Posteriormost angle of posterior iliac crest acute as in *Aquila*; *Spizaëtus ornatus* obtuse and broadly rounded.

Femur

Plate 18, figs. 1 and 1a

Material available—Twenty-three complete, two with broken proximal end, four proximal half, eleven distal half.

Description—In general this element in *grinnelli* is a slender bone, somewhat resembling *Aquila chrysaëtos*, though smaller. It is similar to *Aquila* and *Spizaëtus* as distinguished from *Geranoaëtus* in that (1) the iliac facet narrows on the external side, (2) the trochanter is only slightly raised above the iliac facet, and (3) there is a single orifice on the anterior face of the trochanter.

The distal end differs from *Aquila* in that there is no notch between the internal side of the shaft and the proximal border of the internal condyle; the resemblance is with *Spizaëtus* in this. *Grinnelli* is distinguished from *Spizaëtus ornatus*, however, in its slenderness and in the character of the fibular condyle; this condyle is prominent and roughly outlined, difficult of exact description but differing from any of the other species compared.

Size—See table.

Measurements of Femur

The 21 specimens of this element of *Spizaëtus grinnelli*, which can be measured, fall into nine groups, as follows: 112 mm., 1 specimen; 113 mm., 2 specimens; 115 mm., 3 specimens; 116 mm., 6 specimens; 117 mm., 3 specimens; 118 mm., 1 specimen; 119 mm., 2 specimens; 120 mm., 1 specimen; 121 mm., 2 specimens. The following table includes one specimen from each group.

Specimen	Length	Breadth proximal end	Breadth across condyles	Depth of distal end (internal)	Depth of distal end (external)
	mm.	*mm.*	*mm.*	*mm.*	*mm.*
Spizaëtus grinnelli					
L.A.M.					
No. C625	112.6	24.1	18.5	18.1	19.7
C1362	113.2	24.3	17.6	17.3	19.1
C8363	115.2*a*	25.4	19.6	19.0	21.1
C9270	116.1	25.3	19.7	19.0	21.3
D2183	117.7	26.3	20.8	19.1	21.1
C5269	118.2*a*	27.1	20.5	19.1	21.4
D1811	119.4	26.7	20.9	19.4	22.3
C5163	120.2	26.9	20.1	19.5	21.0
C6554	121.3	27.0	21.2	20.2	22.2
Spizaëtus ornatus					
D. R. Dickey					
No. 16872	91.8	21.3	16.7	16.9	
16929	93.6	21.4	16.5	16.4	17.7
Geranoaëtus					
melanoleucus					
U. S. Nat. Mus.					
No. 18471	102.9	21.9	16.8	17.0	19.0
*233	111.9	22.4	18.4	18.9	20.3

a, approximate. *Collection of L. H. Miller.

TIBIOTARSUS

Plate 19, figs. 1–1b

Material available—Twenty-four complete, eighteen proximal end, seventeen distal end.

Description—Similar to *Aquila* and *Spizaëtus* as distinguished from *Geranoaëtus*: (1) more pronounced rotular crest; (2) anterior margin of inner cnemial crest indented (less than in *Aquila*, however); (3) the anterior of the two scars at the distal extremity of the inner cnemial crest is on the anterior margin, not back of it as in *Geranoaëtus*; (4) position of internal ligamental prominence at distal end, nearer posterior margin of condyle than in *Geranoaëtus*; (5) supratendinal bridge convex; (6) intercondylar sulcus narrow and deep (*Geranoaëtus* broad and shallow).

Similar to *Spizaëtus*: (1) inner cnemial crest less prominent than *Aquila*; (2) intercondylar sulcus deeper and narrower than *Aquila*.

Size—See table.

Measurements of Tibiotarsus

The 24 complete specimens of tibiotarsus of *Spizaëtus grinnelli* fall into 9 groups with regard to length, as follows: 150 mm., 2 specimens; 152 mm., 3 specimens; 153 mm., 1 specimen; 155 mm., 1 specimen; 156 mm., 4 specimens; 157 mm., 7 specimens; 158 mm., 2 specimens; 159 mm., 3 specimens; 164 mm., 1 specimen. The following table includes one specimen from each group.

Specimen	Length	Breadth proximal end	Depth proximal end	Breadth distal end	Depth of external condyle	Depth of internal condyle
	mm.	*mm.*	*mm.*	*mm.*	*mm.*	*mm.*
Spizaëtus grinnelli						
L.A.M.						
No. D1239.....	150.1	18.7	23.6	17.7	12.6	12.3
C7697.....	152.1	18.9	22.8	18.1	13.4	12.8
D213.....	153.0	....	....	18.6	....	....
C1267.....	155.0	....	23.8	18.4	13.7	13.0
C7315.....	156.0	20.0	24.8	19.8	14.0	13.7
C9128.....	157.0	19.4	23.8	19.1	13.5	13.0
C2797.....	158.1	19.7	24.5	19.1	13.8	13.3
C7044.....	159.4	20.0*a*	23.9*a*	19.6	13.7	13.2
C5204.....	164.6	....	....	20.3	....	....
Spizaëtus ornatus						
D. R. Dickey						
No. 16872.....	127.0	16.2*a*	20.4	17.0	11.6	11.8
16929.....	132.0	16.5*a*	20.6	16.9	11.4	11.6
Geranoaëtus						
melanoleucus						
U. S. Nat. Mus.						
No. 18471.....	137.1	16.4	20.8	18.2	11.7	11.4
*233.....	152.9	18.5	23.2	20.3	13.7	12.8

a, approximate. *Collection of L. H. Miller.

TARSOMETATARSUS

Plate 19, figs. 2–2b

Material available—One hundred and four complete; forty chipped and worn; nineteen proximal half; eight distal half.

Description—Upon examination of more specimens than were originally available when the species was described (Miller 1911a), it has been found that many of the characters first referred to are subject to variation, both in the fossil and in the Recent species. The writer has here attempted to present those characters of *grinnelli* which appear constant.

Similar to *Spizaëtus* in general characters. (1) shape: in *Geranoaëtus* sides sloping in abruptly from proximal end, giving appearance of broad proximal end tapering suddenly to slender shaft; in *grinnelli* and *Spizaëtus*, as well as *Aquila*, the narrowing is gradual and less apparent; (2) proportions: shorter and heavier of shaft than *Geranoaëtus*, longer and more slender than *Aquila* (see table); (3) position of tubercle for tibialis anticus: more distal than *Geranoaëtus*, more proximal than *Aquila*; (4) trochleæ weak, particularly well noted in trochlea for digit 3 (also resembling *Geranoaëtus* in weakness of trochleæ) (see table); (5) internal calcaneal ridge more extended distally than *Aquila* or *Geranoaëtus*; (6) knob at end of internal calcaneal ridge long and narrow, in *Geranoaëtus* short and broad (also resembling *Aquila* in this character); (7) inner proximal foramen large and on internal side of calcaneal ridge (also resembling *Aquila* in this character); (8) inner and outer proximal foramina on anterior side close together and at about the same level or with outer more proximal than inner (of the two specimens of *Geranoaëtus* available the foramina in one are far apart, in the other close together—with this variation existing in *Geranoaëtus*, too much weight should not be placed upon this character as diagnostic).

Distinguished from *Spizaëtus ornatus* by (1) internal calcaneal ridge less inclined toward the internal side of the bone, and (2) greater length.

Size—See table of measurements of tarsometatarsus.

Measurements of Tarsometatarsus

Of the 104 complete specimens of this element of *Spizaëtus grinnelli*, 16 were noticeably more slender than the majority. In the following table, four of these slender bones (including their maximum and minimum in length) are given, and a random sample of the larger, more typical specimens (including the maximum and minimum for these also).

Specimen	Length	Breadth proximal end	Breadth distal end	Distance to middle of tubercle for tib. anticus	Depth of trochlea for digit 3	Depth of shaft
	mm.	*mm.*	*mm.*	*mm.*	*mm.*	*mm.*
Spizaëtus grinnelli						
L.A.M.						
No. C7147[1]	100.6	16.8	18.4	19.3	7.4	....
C9759[1]	104.2	16.9	19.7	20.4	7.3	9.1
B9989[1]	106.8	16.9	19.7	21.3	7.4	....
J9857[1]	107.6	17.4	19.8	21.6	7.4	9.5
G2830	102.1	18.7	21.8	22.4	8.3	10.4
G2827	104.4	19.2	22.2	24.0	8.5	9.5
D623	106.6	19.6	22.5	24.4	8.8	10.3
C6804	107.8	19.9	22.0	24.0	8.7	10.0
C6134	109.8	19.4	22.6	24.3	9.3	10.3
C29	111.0	19.4	21.4	24.7	8.2	9.4
C8786	111.7	21.7	23.8	26.6	9.8	11.1
B9538	114.8	19.7	23.0	24.4	8.2	10.0
Spizaëtus ornatus						
D. R. Dickey						
No. 16872	92.0	17.9	19.8	21.3	10.0	10.1
16929	96.8	18.1	20.0	21.9	9.5	9.5
Geranoaëtus melanoleucus						
U. S. Nat. Mus.						
No. 18471	105.0	18.7	20.0	20.7	7.3	8.9
L. H. Miller						
No. 233	114.7	20.7	22.8	22.3	8.8	9.5

[1] Slender specimens.

In studying the elements assigned to *Spizaëtus grinnelli*, it at first seemed possible that there were three species of *Spizaëtus* represented instead of one. In the humerus,

ulna, carpometacarpus and scapula there is a variation in length of 31 mm., 35 mm., 24 mm. and 17.4 mm., respectively, with a decided gap between a small group of very large bones and the remainder of the specimens. In proportions and physical characters, however, it is impossible to distinguish the large elements from the major portion of the specimens. In the leg bones and coracoid, not only is the variation much less—approximately 14 mm. for the tarsometatarsus and tibiotarsus, 11 mm. for the coracoid and 8.7 mm. for the femur—but in all except the tibiotarsus there is no gap from the largest to the smallest specimens; in the tibiotarsus, there is a gap of 4.8 mm. between a single large specimen and the remainder of the bones.

If the size variation in *Spizaëtus* be compared with that noted in the fossil *Aquila chrysaëtos* (see table below), it will be seen that the occurrence of a large range in size is not surprising in a genus related to *Aquila*, and also that a smaller range may be expected in the tarsometatarsus than in the wing elements; the discrepancy in range of size of the other two leg bones as compared with *Aquila* may perhaps be accounted for as a matter of chance due to absence of critical specimens.

Considering the facts relating to these large specimens, the writer does not feel that the evidence justifies the description of a distinct large species of *Spizaëtus*. The reasons for this statement may be briefly summarized as follows: (1) Among the raptores, even in closely related species, the humerus may be expected to vary in some characters other than actual size—this is not the case here; (2) the large range in size is not surprising in a genus related to *Aquila*; (3) the "gaps" in some elements may be accounted for by chance; having less than thirty specimens in all elements except the tarsometatarsus, and less than twenty-five specimens in most cases, the element of chance should be carefully considered.

The range of variation in length of elements of *Aquila chrysaëtos* from Rancho La Brea and of *Spizaëtus grinnelli* is given below.

	Aquila	Spizaëtus
	mm.	*mm.*
Humerus	42.3	31.1 (14 specimens)
Ulna	32.2	35.1 (6 specimens)
Carpometacarpus	20.3	24.4 (28 specimens)
Femur	21.8	8.7 (18 specimens)
Tibiotarsus	24.8	14.5 (24 specimens)
Tarsometatarsus	16.9	14.2 (101 specimens)

The other possibility of a distinct species of *Spizaëtus* was found in taking the relative measurements of the tarsometatarsus. A group of about sixteen tarsometatarsi, among the smaller specimens of this element, were found to be relatively more slender and to have a more proximally placed tubercle for the tibialis anticus muscle than is true of the remaining eighty-five specimens. An attempt to discover a similar condition in the other skeletal elements resulted in finding a single humerus and femur and two tibiotarsi which seemed to agree in combining small size with exceptional slenderness throughout the bone. Each of these, however, overlaps the main group in one or two proportions (see tables). A single small carpometacarpus and small coracoid are separated from the other specimens on the basis of a size gap, but they show no proportional difference.

Though the separation of this smaller group as a distinct species, based upon proportionate differences, seems a more logical proceeding than the separation of the large group just discussed, which could be based only on actual size, the fact that the proportions overlap, and that there is an apparent general tendency to variation in the Aquilinæ has deterred the writer from describing a new species.

The following tables show possible separation of a group of small specimens of *Spizaëtus grinnelli* from the main group.

Humerus

	Length	Length[1] deltoid crest	Breadth[1] distal end	Breadth[1] proximal end	Length[1] bicipital crest	Number of specimens represented
	mm.	*p. ct.*	*p. ct.*	*p. ct.*	*p. ct.*	
Main group						13
Maximum	173.1	38.8	18.3	20.2	19.8	
Minimum	146.2	37.3	17.4	18.5	17.8	
Small specimen						
L.A.M. No. D2626	142.0	37.4	17.8	18.7	17.1	1

Carpometacarpus

	Length	Carpal trochlea		Number of specimens represented
		Greatest breadth[1]	Least breadth[1]	
	mm.	*p. ct.*	*p. ct.*	
Main group				27
Maximum	97.0	27.8	23.8	
Minimum	74.3	24.8	21.6	
Small specimen				
L.A.M. No. E1938	72.6	26.1	22.7	1

Femur

	Length	Breadth proximal end[1]	Breadth across condyles[1]	Depth internal condyle[1]	Depth external condyle[1]	Number of specimens represented
	mm.	*p. ct.*	*p. ct.*	*p. ct.*	*p. ct.*	
Main group						17
Maximum	121.3	22.8	17.6	16.9	18.5	
Minimum	112.6	21.0	16.1	15.3	17.4	
Small specimen						
L.A.M. No. C1362	113.2	21.4	15.5	15.2	16.8	1

Tibiotarsus

	Length	Breadth proximal end[1]	Depth proximal end[1]	Breadth distal end[1]	Number of specimens represented
	mm.	*p. ct*	*p. ct.*	*p. ct.*	
Main group					22
Maximum	164.6	13.1	16.3	12.7	
Minimum	150.1	12.1	14.7	11.5	
Small group					2
L.A.M. No. C3445	152.4	11.4	14.8	11.0	
C5893	150.9	11.7	14.3	11.0	

[1] Ratios, relative to length. Maximum and minimum ratios are given for each measurement of each element in the main group, and of tarsometatarsus in the small group.

	Tarsometatarsus					
	Length	Breadth proximal end[1]	Breadth distal end[1]	Distance to tubercle for tibialis anticus[1]	Depth shaft[1]	Number of specimens represented
	mm.	*p. ct.*	*p. ct.*	*p. ct.*	*p. ct.*	
Main group						85
Maximum.....	114.8	19.4	21.3	23.9	10.1	
Minimum.....	101.1	17.1	19.2	21.2	8.4	
Small group						16
Maximum.....	107.6	17.2	18.9	21.3	8.8	
Minimum.....	100.6	15.8	18.3	19.5	7.9	

[1] Ratios, relative to length. Maximum and minimum ratios are given for each measurement of each element in the main group, and of tarsometatarsus in the small group.

Summary

By way of summarizing the discussion of *Spizaëtus grinnelli* (Miller) which has been presented above, the following table is submitted. This table was prepared before a specimen of Recent *Spizaëtus* became available for comparison. It was originally designed to show the author's reasons for removing *grinnelli* from the genus *Geranoaëtus* and placing it in a genus of closer relationship to *Aquila*. At that time, it appeared necessary to name a new genus for the purpose, since *grinnelli* did not correspond with any genus with which it had been compared. The table is presented here in its original form so that the reader may see how closely *Spizaëtus* accords with the characters necessary for the genus which is to include *grinnelli*. All characters under headings I and II agree with *Spizaëtus* and all but two under heading III; the two exceptions are the carpometacarpus (which may or may not correspond to that of *Spizaëtus*, since there is no specimen with which to make comparison), and the humerus which is distinctive in *grinnelli*. It has been noted previously, in the discussion of the two species of Buteoninæ, that the characters of the humerus are of little generic value.

Table of Relationships of Spizaëtus grinnelli (Miller)

I. Dissimilarities to *Geranoaëtus*[1]

Furcula—furcular process and shape at symphysis
Sternum—sterno-coracoidal impression
Coracoid—furcular facet
Scapula—acromion
Carpometacarpus—symphysis and curved metacarpal III
Pelvis—shape of posterior iliac crest; character of lumbar region
Femur—trochanter, iliac facet, pneumatic opening
Tibiotarsus—intercondylar sulcus, inner cnemial crest, internal ligamental prominence
Tarsometatarsus—shape, hypotarsus, position of tubercle for tibialis anticus

II. Similarities to *Aquila*[2]

Sternum—sterno-coracoidal impression

[1] Characters which exclude *grinnelli* from the subfamily Buteoninæ.
[2] Characters which include *grinnelli* in the subfamily Aquilinæ.

Coracoid—furcular facet
Scapula—acromion
Carpometacarpus—curved metacarpal III
Pelvis—shape of posterior iliac crest
Femur—trochanter, iliac facet, pneumatic opening
Tibiotarsus—intercondylar sulcus (in general character, but with modifications—see below), internal ligamental prominence, inner cnemial crest (in general character, but with modifications—see below)
Tarsometatarsus—shape, hypotarsus (except extent of internal ridge)

III. Dissimilarities to *Aquila*[1]

Furcula—too narrow
Sternum—xiphial area, intermuscular lines
Coracoid—depth of head
Humerus—distinctive
Carpometacarpus—symphysis, tendinal groove
Pelvis—character of lumbar region
Tibiotarsus—deeper, more acute intercondylar sulcus, less prominent inner cnemial crest
Tarsometatarsus—longer, more slender, position of tubercle for tibialis anticus, trochleæ, extent of internal calcaneal ridge

Haliæëtus leucocephalus (Linnæus)

Haliæëtus leucocephalus, though less abundantly represented than *Aquila chrysaëtos*, occurs in greater numbers than any of the extinct species under consideration. Specimens of this species total approximately 1750.

The range in size in the species as represented here, to include both the present *Haliæëtus leucocephalus leucocephalus* and *Haliæëtus leucocephalus alascanus*, has been adequately discussed by Miller (1911a, pp. 310–311). The present study merely provides additional evidence in the matter of measurements of length of separate elements (see measurements of *Haliæëtus* in Tables of Comparative Measurements and Proportions of the Rancho La Brea Eagles and Related Forms on page 79). Briefly, the facts regarding the variation in length of limb bones and coracoid as compared with available specimens of existing subspecies may be expressed in the following figures: Coracoid (fossil) 68.5 mm. to 83.7 mm., (*leucocephalus*) 69.1 mm., (*alascanus*) 80.2 mm.; humerus (fossil) 204.0 mm. to 243.0 mm., (*leucocephalus*) 196.5 mm., (*alascanus*) 228.0 mm.; ulna (fossil) 240.0 mm. to 279.5 mm., (*leucocephalus*) 246.5 mm., (*alascanus*) 264.1 mm.; carpometacarpus (fossil) 103.6 mm. to 128.3 mm., (*leucocephalus*) 107.4 mm., (*alascanus*) 119.7 mm.; femur (fossil) 111.8 mm. to 129.2 mm., (*leucocephalus*) 112.2 mm., (*alascanus*) 126.0 mm.; tibiotarsus (fossil) 150.0 mm. to 174.0 mm., (*leucocephalus*) 157.0 mm., (*alascanus*) 168.5 mm.; tarsometatarsus (fossil) 84.7 mm. to 103.3 mm., (*leucocephalus*) 87.9 mm., (*alascanus*) 97.6 mm.

Since the series of modern skeletons is very limited (only one complete specimen of each subspecies, and one or two incomplete), we can not make accurate comparison of the fossil form with the Recent. Though it is evident that the size range of the former includes some individuals of each subspecies, it is impossible to determine whether the maximum and minimum attained by the two living races combined are

[1] Characters which place *grinnelli* in the genus *Spizaëtus* (exceptions, as noted and explained in discussion above, are carpometacarpus and humerus).

in accordance with the extremes noted for the species as represented in the Rancho La Brea deposits.

Though *Haliæëtus* is not uncommon in the fossil record of North America, it is recorded only from the Pleistocene and is represented by no species other than *leucocephalus*. The localities in which fossils of this species have been found are as follows: Rancho La Brea, McKittrick, San Pedro and Carpinteria, California; Fossil Lake, Oregon; Sheridan County, Nebraska; Conkling Cavern, New Mexico; Sabre-tooth Cave, Seminole Field, Venice and Melbourne, Florida.

SUBFAMILY ÆGYPIINÆ

There are two genera of raptores from Rancho La Brea which show affinity with the Old World Vulture subfamily, Ægypiinæ; these are *Neogyps* and *Neophrontops*. Both genera were assigned to the Old World Vultures when first described by Miller (1916) from the tarsometatarsus only. The present study of nearly the entire skeleton has yielded still further evidence in support of Miller's contention.

While *Neogyps* is undeniably eagle-like in certain of the more adaptive characters, it is, at the same time undeniably ægypiine in other characters, of apparently greater genetic value.

Neophrontops shows its ægypiine affinities in every characteristic element, exhibiting in nearly all of the principal skeletal parts the resemblance to *Neophron* which characterizes the tarsometatarsus.

It seems appropriate at this time, also, to again consider the status of *Palæoborus umbrosus* Cope from the Miocene of New Mexico. This species is the only North American fossil species, other than *Neogyps* and *Neophrontops* to have been assigned to the Old World Vultures. The discussion of *Palæoborus* follows that of *Neophrontops*.

Neogyps errans Miller

Plates 20 to 25

Neogyps errans Miller, Univ. Calif. Publ. Bull. Dept. Geol., 9, 108–109, fig. 2, 1916.

To date, *Neogyps* has been described only from the tarsometatarsus. On the basis of characters of this bone, the genus was assigned to the family Vulturidæ,[1] with closest resemblance to *Gypaëtus barbatus* (Miller, 1916, p. 109).

The present study has included all of the principal elements of the skeleton. Miller's assignment of *Neogyps* to the Old World Vulture group, based upon the tarsometatarsus, is corroborated by this study, though, as will be seen in the descriptions to follow, each individual element could not be so assigned.

[1] Here considered not as a family, but as a subfamily (Ægypiinæ) under the Accipitridæ.

Cranium

Plate 20, figs. 1 and 1a

Material available—Nineteen specimens, of which three are fragmentary.

Description—In general appearance a broad, flat cranium (relative breadth and height, compared to modern forms, shown in the following table), with rugged contours as in the eagles, and to a lesser extent *Gypaëtus*. Marked indentation in median dorsal line, extending from anterior end of frontals posteriorly past crown of skull occipital region deeply furrowed and temporal fossa broad and heavily margined. This evidence of a powerful temporal muscle is reflected also in the strong lower jaw.

Measurements of Cranium

Specimen	a Breadth across postorbital processes	b Depth	Ratio of b to a
	mm.	*mm.*	*p. ct.*
Sarcogyps calvus L.A.M. No. 226	51.7	39.1	75.5
Neophron percnopterus L. H. Miller No. 227	44.5	33.1	74.3
Ægypiinæ, species? L.A.M. No. 232	67.4	45.4	67.3
Gypaëtus barbatus L. H. Miller No. 263	70.4	44.4	63.1
Haliæëtus leucocephalus L.A.M. No. 291	67.4	40.0	59.3
Aquila chrysaëtos L.A.M. No. 468	61.9	40.3	65.1
Geranoaëtus melanoleucus L. H. Miller No. 233	62.8	36.5	58.1
Neogyps errans L.A.M. No. C2053	75.4	41.3	54.7

ROSTRUM

Plate 20, figs. 2 and 2a

Material available—Thirteen specimens (one of anterior tip only).

Description—It is scarcely possible to designate characters of this element which would serve, in all cases, to separate the Ægypiinæ from the eagles. Though the narrow, vertically placed external narial openings are peculiar to the vultures, the larger openings (similar to the eagles) are also found in this group.

There is apparently a constancy in the relatively greater length and less breadth of the rostrum of the ægypiines as compared with the eagles. The rostrum of *Neogyps* is narrow, but not as narrow as in the Ægypiinæ, being closer to *Haliæëtus* or *Urubitinga*. Another character which appears to be of some value in separating the vultures from the eagles is that in the latter the anterior portion of the tomia is never on a line with the inferior border of the external nares, but is always a considerable distance below; in the vultures the tomia anteriorly are on a line with or only slightly below the inferior border of the nares; of the vultures examined, *Gypaëtus* is the most eagle-like in this regard. In *Neogyps* the edge is even lower than in *Gypaëtus*, and more closely approximates *Aquila*.

Dorsally, in the vultures, there is a depression or break between the anterior end of the nasal processes of the premaxillaries and the beginning of the beak. In the eagles, though a slight depression may be present, the general effect is of a gradual curve from the nasal portion to the tip of the beak; *Neogyps* resembles the eagles in this character.

Measurements of Rostrum

Specimen	a Length[1]	b Breadth[2]	c Height[3]	Ratio of b to a
	mm.	*mm.*	*mm.*	*p. ct.*
Sarcogyps calvus				
L.A.M.				
No. 226	42.4	24.3	20.4	57.3
Neophron percnopterus				
L. H. Miller				
No. 227	40.1	13.9	6.3	34.6
Ægypiinæ, species?				
L.A.M.				
No. 232	40.7	22.3	22.5	54.7
Gypaëtus barbatus				
L. H. Miller				
No. 263	47.3	24.2	19.6	51.1
Haliæëtus leucocephalus				
L.A.M.				
No. 291	41.6	28.4	26.6	68.2
Aquila chrysaëtos				
L. H. Miller				
No. 421	30.7	22.8	19.9	74.2
Geranoaëtus melanoleucus				
L. H. Miller				
No. 233	28.6	24.2	15.8	84.2
Urubitinga anthracina				
D. R. Dickey				
No. 16950	20.0	13.8	9.9	69.0
Neogyps errans				
L.A.M.				
No. J9063	35.0	22.9	20.1	64.0
D1076	35.0	22.6	21.8	64.5
D4615	36.3	22.7	22.3	62.5
H9062	37.0	23.1	21.9	62.4

[1] Measured from angle formed by lateral branch of nasal joining maxillary.
[2] Measured below this angle.
[3] Measured at junction of nasal process of premaxillary with beak.

Mandible

Plate 20, fig. 4

Material available—Nineteen specimens (only one complete).

Description—The vulture mandible is distinguished from that of the eagles by its frailty, as exhibited by the thin, high rami.

As may be noted in the following table, *Neogyps* falls with the eagles in this respect.

Measurements of Ramus

Specimen	a Height	b Breadth	Ratio of b to a
	mm.	*mm.*	*p. ct.*
Sarcogyps calvus			
L.A.M.			
No. 226	11.0	2.5	22.7
Neophron percnopterus			
L. H. Miller			
No. 227	5.8	1.6	27.6
Ægypiinæ, species?			
L.A.M.			
No. 232	10.1	2.5	24.7
Gypaëtus barbatus			
L. H. Miller			
No. 263	14.8	1.8	12.1
Haliæëtus leucocephalus			
L.A.M.			
No. 291	10.6	3.2	30.1
Aquila chrysaëtos			
L. H. Miller			
No. 421	9.1	2.8	30.7
Geranoaëtus melanoleucus			
L. H. Miller			
No. 233	7.6	2.8	36.8
Neogyps errans			
L.A.M.			
No. D323	8.3	2.9	34.9
C694	9.0	2.7	33.3
C2218	9.0	3.5	38.8
C3263	9.3	3.2	34.3
C491	9.3	2.7	34.4
C5233	9.5	2.9	30.5

STERNUM

Plate 21, figs. 1 and 1a

Material available—Seventeen specimens, two of which are complete.

Description—The characters of the sternum of the modern vultures, as distinguished from the eagles, are as follows: (1) Broad ventral manubrial spine; (2) low carina; (3) short and broad sterno-coracoidal impression. With respect to the first character, *Neogyps* is vulture-like, being closest to *Gypaëtus* and to specimen No. 232; *Neogyps* agrees with the vultures in the second character, also, though the carina does not curve decidedly upward at the anterior end as in *Gypaëtus*, *Sarcogyps* and ægypiine specimen No. 232, being more like *Neophron* in this respect; in the shape of sterno-coracoidal impression, *Neogyps* is individual, being long and narrow, with almost parallel sides; the impression in the eagles is longer than in the vultures, but differs from *Neogyps* in other respects (in *Aquila* and *Geranoaëtus* it is too broad, and in *Haliæëtus* the sides are not so nearly parallel).

Measurements of Sternum

Specimen	a Breadth across ventral lips of coracoidal sulcus	b Breadth of manubrium	Ratio of b to a
	mm.	*mm.*	*p. ct.*
Sarcogyps calvus			
L.A.M. No. 226	52.1	9.7	18.6
Neophron percnopterus			
L. H. Miller No. 227	38.1	6.9	18.1
Ægypiinæ, species?			
L.A.M. No. 232	52.9	11.5	21.7
Gypaëtus barbatus			
L. H. Miller No. 263	72.1	15.6	21.6
Haliæëtus leucocephalus			
L.A.M. No. 32	46.5	6.2	13.3
Aquila chrysaëtos			
L. H. Miller No. 471	47.2	7.4	15.6
Geranoaëtus melanoleucus			
L. H. Miller No. 233	39.8	7.1	17.8
Neogyps errans			
L.A.M. No. C4136	43.7	9.2	21.1
D4385	45.0	9.8	21.7
C1118	46.4	11.0	23.7
C9911	48.0	9.4	19.6

Furcula

Plate 20, figs. 3 and 3a

Material available—Twenty-five specimens (one complete, two with one clavicle broken, five symphyses with sides broken, seventeen ends).

Description—The furcula in *Neogyps* is curved backward and slightly upward near the symphysis, as in the eagles, though to a lesser degree; this region straight in the vultures, except *Neophron*, and even in this genus the curvature is less than in *Neogyps*. Symphysis broad, as in Ægypiinæ; furcular process larger at apex of symphysis than posteriorly, as in Ægypiinæ and *Haliæëtus*. Coracoidal facet tending to be long and narrow as in *Sarcogyps* and specimen of vulture No. 232. Arch narrower than in *Haliæëtus*.

Coracoid

Plate 21, figs. 2 and 2a

Material available—Forty specimens, thirty-one of which are complete.

Description—In general appearance similar to the vultures (with the exception of *Neophron*) in the decided projection of the furcular facet, on the ventral edge, over the body of the bone. A relatively shorter and stockier bone than in any of the vultures or eagles examined. Distance from sternal facet to procoracoid relatively less than in the eagles and *Gypaëtus* (see table).

Measurements of Coracoid

Specimen	a Length	b Distance from sternal facet to procoracoid	Ratio of b to a
	mm.	*mm.*	*p. ct.*
Sarcogyps calvus			
L. H. Miller			
No. 226	77.8	44.3	56.6
Neophron percnopterus			
L. H. Miller			
No. 227	50.5	28.7	56.8
Ægypiinæ, species?			
L.A.M.			
No. 232	73.8	40.3	54.6
Gypaëtus barbatus			
L. H. Miller			
No. 263	88.3	57.7	65.3
Haliæëtus leucocephalus			
L.A.M.			
No. 32	75.2	44.6	59.3
Aquila chrysaëtos			
L. H. Miller			
No. 471	72.1	44.4	61.5
Geranoaëtus melanoleucus			
L. H. Miller			
No. 233	61.2	38.8	63.4
Neogyps errans[1]			
L.A.M.			
No. C1096	65.9	38.3	58.1
C3145	66.7	38.2	57.2
C1981	67.7	38.0	56.1
C3330	68.3	39.9	58.4
D882	69.9	40.4	57.7

[1] In selecting specimens of *Neogyps* for measurement, the extremes (large and small) were taken, and a random sample of intermediate sizes.

Scapula

Plate 21, figs. 3 and 3a

Material available—Forty-four specimens.

Description—A characteristic of *Neogyps*, which separates it from any specimen of eagle available, is a large pneumatic foramen in the middle of the ventral side immediately posterior to the proximal articular surface. In the subfamily Ægypiinæ, *Neophron* and *Sarcogyps* lack such a foramen; in specimen No. 232 there is a suggestion of a small foramen or foramina, in a similar position; and in *Gypaëtus* there is a well-marked foramen on the ventral side, but in the acromial region. Another characteristic of *Neogyps*, which distinguishes this genus from all other specimens examined, with the exception of *Gypaëtus*, is the lack of pneumatic foramina on the anterior surface of the acromion.

In height of acromion relative to breadth of anterior end, *Neogyps* is nearer *Aquila* and *Geranoaëtus* than any of the vultures, or *Haliæëtus*.

Measurements of Scapula

Specimen	a Breadth of anterior end	b Breadth of acromion	Ratio of b to a
	mm.	*mm.*	*p.ct.*
Neophron percnopterus			
L. H. Miller			
No. 227	14.3	9.7	67.8
Ægypiinæ, species?			
L.A.M.			
No. 232	19.5	15.5	79.4
Gypaëtus barbatus			
L. H. Miller			
No. 263	22.2	14.7	66.2
Haliæëtus leucocephalus			
L.A.M.			
No. 32	19.4	13.9	71.6
Aquila chrysaëtos			
L. H. Miller			
No. 471	19.9	11.5	52.7
Geranoaëtus melanoleucus			
L. H. Miller			
No. 233	17.7	10.0	56.4
Neogyps errans			
L.A.M.			
No. H6286	17.5	8.7	50.8
D1007	18.7	10.1	54.0
C4594	19.0	10.9	57.3
C664	19.2	10.7	55.7
C1164	20.5	11.9	57.0

Humerus

Plate 22, figs. 1 and 1a

Material available—Twenty-six proximal end, twenty-three distal end, fifteen complete.

Description—Proximal end: relatively shorter deltoid crest than in any modern form measured (see table). Anconal side, region from median crest to deltoid crest not flattened as in Ægypiinæ, nor angular as in *Geranoaëtus*; nearer *Aquila* or *Haliæëtus*, somewhat intermediate between these two. Pneumatic foramen narrower than long, as in *Aquila* and *Geranoaëtus*, but fossa of less extent distally than in these species, thus nearer the vultures and *Haliæëtus*.

Distal end: in the Ægypiinæ flaring almost equally to each side of shaft; in *Aquila* and *Geranoaëtus* flare greater on internal side; *Haliæëtus* intermediate between the vultures, and *Aquila* and *Geranoaëtus*; *Neogyps* closest to *Haliæëtus*. Impression of brachialis anticus broad and deep as in the vultures, and, to a less extent, *Haliæëtus*.

Shaft: curved slightly, as in vultures (with the exception of *Gypaëtus* in which it is nearly straight) and *Haliæëtus*.

Measurements of Humerus

Specimen	a Length	b Breadth proximal end	c Length deltoid crest	d Breadth of distal end	Ratio b to a	Ratio c to a	Ratio d to a
	mm.	*mm.*	*mm.*	*mm.*	*p. ct.*	*p.c t.*	*p. ct.*
Sarcogyps calvus							
L.A.M.							
No. 226	212.4	37.5	78.8	35.2	17.6	37.5	16.5
Neophron percnopterus							
L. H. Miller							
No. 227	145.6	27.5	54.2	23.3	18.8	37.2	16.0
Ægypiinæ, species?							
L.A.M.							
No. 232	199.8	38.2	75.8	34.6	19.1	37.9	17.3
Gypaëtus barbatus							
L. H. Miller							
No. 263	241.9	48.7	91.8	39.3	20.1	37.9	16.2
Haliæëtus leucocephalus							
L.A.M.							
No. 291	228.0	41.8	88.2	38.2	18.3	38.6	16.7
Geranoaëtus melanoleucus							
L. H. Miller							
No. 233	160.0	32.0	61.8	28.8	20.0	38.6	18.0
Neogyps errans							
L.A.M.							
No. C4549	199.0	36.5	69.2	33.3	18.3	34.7	16.7
C1997	202.8	37.2	71.8	32.6	18.3	35.4	16.0
C1803	205.1	37.7	70.0	33.6	18.3	34.1	16.3
C4507	206.1	37.7	70.0	32.7*a*	18.0	33.9	15.8
C4780	207.6	37.7	73.3	33.7	18.1	35.3	16.2
C2946	208.2	37.2	73.8	34.0	17.8	35.4	16.7
B8426	214.5	41.1	76.0	36.5	18.6	35.4	16.1
C6416	215.4	39.8*a*	77.2	34.5	18.4	35.8	16.0
B8477	217.6	....	....	....	....	....	....

a, approximate.

Ulna

Plate 23, figs. 1–1b

Material available—Six complete, twenty proximal end, thirty-four distal end.

Description—Similar in general appearance to Ægypiinæ. This similarity is noted particularly in the narrowing of the palmar side of the shaft near the proximal end, and in the relatively short external condyle at the distal end (see table).

Measurements of Ulna

Specimen	a Length	b Breadth of palmar side of shaft near proximal end	c Height of external condyle	Ratio of b to a	Ratio of c to a
	mm.	*mm.*	*mm.*	*p. ct.*	*p. ct.*
Sarcogyps calvus					
L.A.M.					
No. 226	274.9	11.6	18.0	4.2	6.5
Neophron percnopterus					
L. H. Miller					
No. 227	171.6	7.2	10.4*a*	4.1	6.0
Ægypiinæ, species?					
L.A.M.					
No. 232	280.2	11.9	16.7	4.2	5.9
Gypaëtus barbatus					
L. H. Miller					
No. 263	275.0	11.3	18.4	4.1	6.6
Haliæëtus leucocephalus					
L.A.M.					
No. 291	264.1	13.5	19.5	5.1	7.3
Aquila chrysaëtos					
L. H. Miller					
No. 421	223.0	11.6	19.7	5.2	8.8
Geranoaëtus melanoleucus					
L. H. Miller					
No. 233	189.4	10.0	16.7	5.2	8.8
Neogyps errans					
L.A.M.					
No. C8378	236.0	10.3	14.8	4.3	6.2
C2322	240.0	11.0	15.5	4.5	6.4
C2995	251.7	11.2	16.8	4.4	6.6

a, approximate.

Radius

Plate 23, figs. 2 and 3

Material available—Six proximal ends. No complete radius ascribable to *Neogyps* has been found. Since the distal end of this element is not reliably diagnostic, identification of that part of the radius is omitted here, though a specimen, presumably of this species, is figured (Plate 23, fig. 3).

Description—Shaft slender; capital tuberosity narrow and prominent as in *Haliæëtus* or *Geranoaëtus*. Character of ligamental papilla variable, but, in some individuals similar to ægypiine specimen No. 232. For further characteristics, the reader is referred to Plate 23, figures 2 and 2a.

Carpometacarpus

Plate 22, fig. 2

Material available—Nineteen complete, forty-four with metacarpal III broken.

Description—The carpometacarpus assigned to *Neogyps* (the reasons for this assignment are described under Methods of Identification of Material, p. 12) is unlike any other species at hand, Recent or Pleistocene. The Recent species most nearly resembled in various characters are listed below:

Internal side of distal end of M III with deep, rounded indentation	Nearest *Sarcogyps* (not identical)
Pneumatic foramina lacking	Eagles, *Gypaëtus*, *Neophron*
Height of internal crest of trochlea (less than any other species measured)	Nearest *Neophron*
Height of M I relative to least breadth of proximal end, approximately 63 per cent	Nearest *Geranoaëtus*, *Haliæëtus* and *Neophron*
Length (average, 105.8 mm.)	Nearest *Aquila*, *Sarcogyps* and vulture No. 232.

Measurements of Carpometacarpus

Specimen	a Length	b Greatest depth of proximal end	c Least depth of proximal end	d Height carpal end[1]	Ratio b to a	Ratio c to a	Ratio d to a
	mm.	*mm.*	*mm.*	*mm.*	*p. ct.*	*p. ct.*	*p. ct.*
Sarcogyps calvus L.A.M. No. 226.....	107.6	26.2	22.9	24.3	24.3	21.2	22.5
Neophron percnopterus L. H. Miller No. 227.....	77.9	18.7	16.8	17.0	24.0	21.5	21.8
Ægypiinæ, species? L.A.M. No. 232.....	106.3	26.1	23.4	25.0	24.5	22.0	23.5
Gypaëtus barbatus L. H. Miller No. 263.....	122.8	31.5	27.8	27.4	25.6	22.6	22.3
Haliæëtus leucocephalus L.A.M. No. 291.....	119.7	29.2	26.2	24.7	24.3	21.8	20.6
Aquila chrysaëtos L. H. Miller No. 421.....	103.4	26.0	22.9	21.0	25.0	21.1	20.3
Geranoaëtus melanoleucus L. H. Miller No. 233.....	87.6	23.0	20.1	17.5	26.2	22.9	19.9
Neogyps errans L.A.M. No. C5482.....	98.4	25.1	22.4	19.4	25.5	22.7	19.7
B9642.....	101.1	25.8	22.8	20.3	25.5	22.5	20.0
B8551.....	105.3	27.8	24.6	22.7	26.4	23.3	21.5
D2465.....	110.6	27.3	25.2	23.2	24.6	22.7	20.9
C6482.....	111.5	28.0	24.7	23.2	25.1	22.1	20.8

[1] Measurement taken from external crest of carpal trochlea to pollical facet.

Pelvis

Plate 24, figs. 1–1b

Material available—Two complete with synsacrum, one synsacrum with part of pelvis, three posterior portion of pelvis only.

Description—The shape of the arch at the posterior end of the pelvis, from the tip of the ischium on one side to the tip of the ischium on the other side, is apparently a reliable diagnostic character among the accipitrids. In the Ægypiinæ the arch is broad and low and evenly rounded; in *Haliæëtus* it is evenly rounded, but is narrow and high; in the other eagles the arch is uneven, narrowing at about the junction of the ilium and ischium, posteriorly and then flaring outward in the ischial portion. The arch in *Neogyps* has a still different variation—it does not narrow in before the final flare of the ischium, but flares gradually to the junction of ischium and ilium, where it turns outward slightly to increase the flare. The span is narrower than in the ægypiines, but of about the same height.

The ilio-ischiatic fenestra in the ægypiines is distinctly outlined externally with the internal margin of the ischium not in evidence in the region of the fenestra, when viewed laterally; the external border is indistinct in the eagles, with the internal margin of the ischium extending from the posterior border of the fenestra, internally, dorsally and anteriorly so that the attachment to the synsacrum is visible through the fenestra in lateral view; internal margin of ischium less evident in *Haliæëtus* than in other eagles examined; *Neogyps* closest to *Haliæëtus*.

Illo-ischiatic fenestra in ægypiines of greater extent anteroposteriorly than in eagles, extending well posterior to the obturator foramen. The extent is slightly less in *Gypaëtus* than in the other ægypiines examined. In the eagles the fenestra extends posteriorly to or only slightly beyond the posterior border of the obturator foramen. In *Neogyps* the fenestra is larger than in the eagles, though smaller than in the vultures, and in extent posterior to the obturator foramen is intermediate between *Gypaëtus* and *Haliætëus*.

Posterior iliac crest in ægypiines running almost straight posteriorly; in *Haliæëtus* it is slightly and evenly rounded; in *Aquila* and *Geranoaëtus* it is uneven. Unfortunately, no specimen of *Neogyps* is complete in this region, but a curved border is visible, which apparently does not assume the uneven contour of *Aquila* or *Geranoaëtus*, but resembles *Haliæëtus* more closely. *Haliæëtus* is different from *Neogyps*, however, as well as from the other eagles examined, in the rounding, indefinite edges of the crest, throughout its length. Posteriorly, in *Neogyps*, the dorsal face and internal side of the lateral face of the ilium are distinctly separated, the ilium turning at a definite angle; this condition is also very marked in the ægypiines and to less extent in *Aquila* and *Geranoaëtus;* in *Haliæëtus*, however, the junction of the two surfaces is rounded so that there is no definite point of distinction between them.

The transverse processes of the synsacral thoracic and lumbar vertebræ are markedly pneumatic. This is also true of the processes in the vultures. The eagles appear less pneumatic.

FEMUR

Plate 25, figs. 2-2b

Material available—Nineteen complete, seventeen distal end, three proximal end.

Description—In the Ægypiinæ the trochanteric crest is short proximodistally, but deep anteroposteriorly. In the eagles, it is longer and less flaring. *Neogyps* is short as in the vultures, but in depth it is no greater than the eagles. Anteriorly the crest appears distinct from the proximal part of the shaft in the ægypiines, while in the eagles the two are merged; *Neogyps* is like the vultures.

Other characters of the *Neogyps* femur, which, however, seem to have no taxonomic importance, are: (1) head of medium size with a fairly shallow, pit-like attachment of the round ligament; (2) single anterior foramen; (3) muscle scar of the posterior side at the distal end, single and distinctly outlined, small in extent, but considerably raised; situated above the popliteal area, slightly external to the median line.

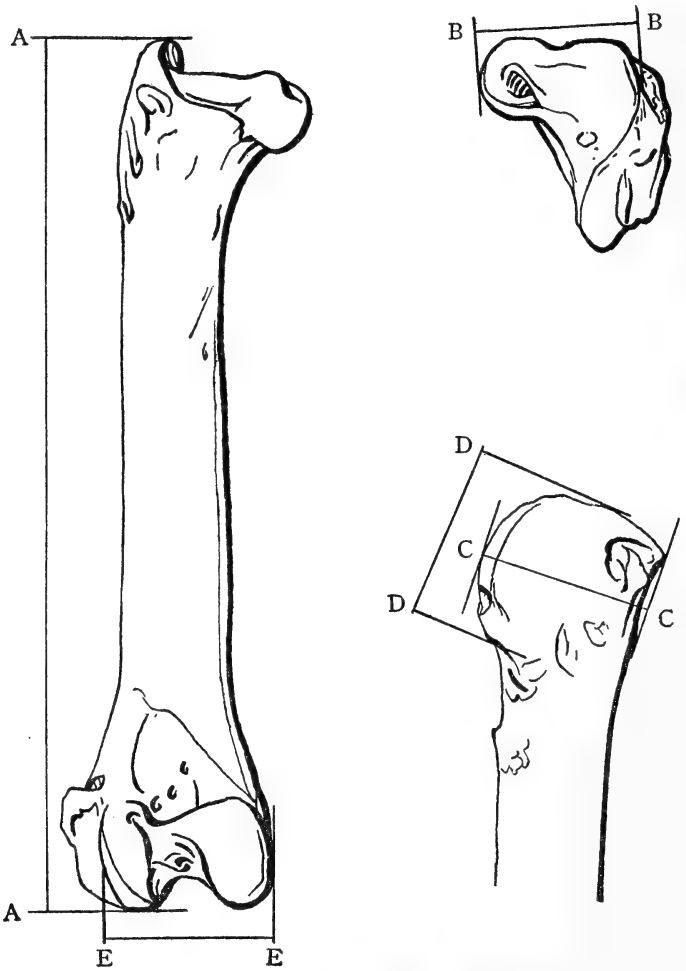

FIG. 3—Drawings of the femur of *Sarcogyps calvus* showing positions of measurements of this element given in tables under *Neogyps errans* and *Neophrontops americanus*.

Measurements of Femur[1]

Specimen	a Length	b Breadth proximal end	c Depth through troch-anteric ridge	d Length of troch-anteric ridge	e Breadth distal end across condyles	Ratio c to b	Ratio d to b	Ratio b to a	Ratio e to a
	mm.	*mm.*	*mm.*	*mm.*	*mm.*	*p. ct.*	*p. ct.*	*p. ct.*	*p. ct.*
Sarcogyps calvus L.A.M. No. 226.....	112.4	21.0	23.7	23.4	21.6	112.3	111.1	18.6	19.2
Neophron percnopterus L. H. Miller No. 227.....	70.9	14.4	13.3	14.7	14.1	92.3	121.4	20.3	19.8
Ægypiinæ species? L.A.M. No. 232.....	104.3	20.5	20.4	24.0	20.0	99.5	117.0	19.6	19.1
Gypaëtus barbatus L. H. Miller No. 263.....	125.0	24.8	26.8	32.4	25.3	108.0	130.6	19.8	20.2
Haliæëtus leucocephalus M.V.Z. No. 8326.....	126.0	22.5	21.6	33.6	22.0	96.0	149.3	17.8	17.4
Aquila chrysaëtos M.V.Z. No. 50475.....	128.9	21.0	20.1	33.1	22.5	95.5	157.5	16.2	17.4
Urubitinga anthracina D. R. Dickey No. 16950.....	71.8	11.1	10.0	16.6	11.8	90.0	149.5	15.4	16.4
Neogyps errans L.A.M. No. C9098.....	103.4	18.5	17.5	21.0	19.1	94.5	113.0	17.8	18.4
C4212.....	106.3	18.8	17.8	21.1	19.4	94.5	112.0	17.6	18.2
C3212.....	107.2	18.7	17.4	20.0	18.0	93.0	107.0	17.4	16.7
C6762.....	113.4	20.8	19.6	25.6	20.7	94.3	123.0	18.3	18.2

[1] See text figure 3, for positions of measurements.

Tibiotarsus

Plate 25, figs. 1–1b

Material available—Twenty-four complete, nine proximal end, fourteen distal end.

Description—The proximal end of the tibiotarsus of the Ægypiinæ is differentiated from the Aquilinæ and Buteoninæ by a shortening of the flaring portion of the inner cnemial crest so that it narrows abruptly; in the eagles, the crest is longer and narrows gradually. The distal extremity of the crest is less definitely marked in the Ægypiinæ than in the other subfamilies under consideration. *Neogyps* shows closer relationship with the vultures than with the eagles in the characters of the crest, though the distal extremity is more definitely marked.

The distal end of the tibiotarsus in the Ægypiinæ differs from the Aquilinæ and Buteoninæ in greater depth relative to breadth. *Neogyps* resembles the eagles in this respect, although some individuals of *Neogyps* agree with *Neophron*, whose depth is less than the average for the ægypiines.

The supratendinal bridge is more horizontally placed in the ægypiines than in the eagles. In *Neogyps*, the angle of the bridge is intermediate—more vertical than the vultures, more horizontal than the eagles.

Measurements of Tibiotarsus

Specimen	a Length	b Breadth proximal end	c Depth proximal end	d Breadth distal end	e Depth distal end	Ratio e to d
	mm.	*mm.*	*mm.*	*mm.*	*mm.*	*p. ct.*
Sarcogyps calvus L.A.M. No. 226	158.9	20.1	26.0	20.2	17.1	84.6
Neophron percnopterus L. H. Miller No. 227	117.4	13.5	17.4	14.6	10.6	72.6[1]
Ægypiinæ, species? L.A.M. No. 232	159.4	20.5	23.5	19.1	15.0	78.5
Gypaëtus barbatus L. H. Miller No 263	170.9	24.4	31.6	22.3	17.6	79.0
Haliæëtus leucocephalus L.A.M. No. 291	166.5	23.2*a*	28.9	23.2	16.6	71.6
Aquila chrysaëtos M.V.Z. No. 50475	164.0	23.0	27.3	22.7	16.5	72.6
Geranoaëtus melanoleucus L. H. Miller No. 233	152.9	18.5	23.2	20.3	13.6	67.0
Neogyps errans L.A.M. No. C3492	140.9	19.9	22.8	19.2	13.6	70.6
D610	141.6	18.8*a*	22.5	18.0	13.3	73.8
C5218	145.0	21.0	24.2	19.9	14.1	70.7
D1091	145.2	21.2	24.1	19.6	13.7	69.8
C2199	146.2	20.5	23.0*a*	20.6	13.9	67.5
D3531	148.5	20.5	24.0	19.1	13.2	69.0
B9302	153.6	20.5*a*	23.4*a*	20.8	13.7*a*	65.7*a*

[1] This ratio 77 per cent in L.A.M. specimen No. 239.
a, approximate.

Tarsometatarsus

Plate 24, figs. 2 and 2a

Material available—One hundred eight complete, fourteen incomplete.

Description—A description of this element has been given by Miller (1916, pp. 108–109) and the following discussion is only by way of addition thereto.

Miller remarks that one of the vulturine characters of *Neogyps* is the weak internal calcaneal ridge of the hypotarsus. After a study of the tarsometatarsus of the various modern species available and particularly of *Sarcogyps*, in which species both ridges are well developed, it is the present writer's opinion that the distinctive feature of the vulture hypotarsus is not so much the weakness of one or the other of the calcaneal ridges, as the diminishing in size of the tendinal canal between. This may be associated with a decrease in size of the flexor tendons. Aside from the closer proximity of the two ridges, in the vultures, the lessened size of the canal is brought about by the raising of the shaft between and distal to the calcaneal ridges, so that a decided convexity is present; with regard to this character, *Neogyps* is immediately set apart from *Aquila* and *Geranoaëtus;* however, it does not exhibit the marked convexity characteristic of the vultures; it, perhaps, more closely approximates *Haliæëtus*, though it is not identical with that genus. The proximity of the two ridges in *Neogyps* is approximately as in the vulture specimen, No. 232. The shape of the internal

Measurements of Tarsometatarsus

Specimen	a Greatest length	b Length to middle of tubercle for tibialis anticus	c Breadth proximal end	d Breadth distal end	e Depth trochlea digit 2	f Depth trochlea digit 3	g Depth trochlea digit 4	Ratio e to d	Ratio f to d	Ratio g to d	Ratio f to e	Ratio f to g
	mm.	*mm.*	*mm.*	*mm.*	*mm.*	*mm.*	*mm.*	*p. ct.*	*p. ct.*	*p. ct.*	*p. ct.*	*p. ct.*
Sarcogyps calvus												
L.A.M.												
No. 226	95.5	20.1	21.2	23.7	12.4	12.2	13.2	51.9	51.4	55.6	98.3	92.4
Neophron percnopterus												
L. H. Miller												
No. 227	81.3	14.8	14.7	16.8	8.7	7.4	8.5	51.3	44.0	50.1	85.0	87.0
Ægypiinæ, species?												
L.A.M.												
No. 232	108.4	18.9	20.0	23.6	12.8	11.2	12.8	54.2	47.4	54.2	87.5	87.5
Gypaëtus barbatus												
L. H. Miller												
No. 263	99.5	22.3	24.1	24.9	13.0	12.3	13.7	51.0	49.3	55.0	94.6	89.7
Haliæëtus leucocephalus												
L.A.M.												
No. 291	97.6	25.2	24.1	26.7	15.2	11.1	13.6	56.9	40.0	50.9	73.0	81.6
Aquila chrysaëtos												
L. H. Miller												
No. 421	99.9	27.3	24.7	26.6	15.4	11.0	14.8	57.8	41.3	55.6	71.4	74.3
Geranoaëtus melanoleucus												
L. H. Miller												
No. 233	114.7	21.3	20.5	22.4	12.8	8.6	12.2	57.1	38.3	54.4	67.1	70.4
Neogyps errans												
L.A.M.												
No. C5576	84.0	19.8	18.5	21.4	11.1	9.0	10.5	51.8	42.0	49.0	81.0	85.7
B8350	86.1	20.3	19.7	21.7	11.9	9.3	11.3	54.8	42.9	52.0	78.1	82.2
C1934	88.8	20.3	21.3	23.0	12.5	9.4	11.5	54.3	40.8	50.0	75.2	81.7
D8390	93.0	23.1	21.2	24.1	12.6	9.6	11.2	52.2	39.8	46.4	76.1	85.7

calcaneal ridge, and the position of the internal foramen as seen in lateral view, agree with *Sarcogyps* (a short ridge, tilted toward the median line, with the foramen on the internal side of the ridge); the position of the foramen is the same in the other vultures, but the ridge is, in many cases, smaller.

The absence of scars for the attachment of the ligamental bridge, under which passes the tendon of the extensor longus digitorum, characterizes the ægypiines as distinguished from the eagles. This condition, which doubtless accompanies a lessening of the ability to extend the digits, is in keeping with the vulturine habits of the former group; in the eagles the digits must be widely extended as the bird prepares to grasp its prey, and again strong digital extension is required in releasing the grasp. In *Neogyps* the scars are distinct, indicating the presence of a fairly strong ligamental bridge, probably accompanied by powers of digital extension equal to many of the eagles.

At the distal end, the trochlea for digit 3 in the vultures is larger, both in proportion to breadth of distal end and to size of the other trochleæ, than in the eagles. Accompanying this increase in size of the median trochlea, is a less-marked decrease in size of the trochlea for digit 2. The size of the trochlea for digit 4 is not a subfamily characteristic. In *Neogyps* the breadth of the trochlea for digit 3 relative to breadth of distal end is as in the eagles, though the breadth of this trochlea relative to those for digits 2 or 4 is intermediate between the eagles and the vultures. The trochlea for digit 2 in *Neogyps* is small relative to the breadth of the distal end, as in the vultures.

Conclusions Regarding *Neogyps errans*

Neogyps errans was a large raptorial bird with relatively short legs and long wings. The head is broad and low, the rostrum short, high and sharp, and the mandible stout. The feet, though small and weak compared with *Aquila*, show evidence of stronger musculature than do the vulture feet. In these characters of head and feet, *Neogyps* appears at first glance to be closer to the eagles than to the vultures.

It is important, however, that characters which reflect the habits of the bird should not be confused with those of genetic value. Characters of the head and feet are naturally most apt to be modified by adaptations and, therefore, to be the ones in which the greatest differences between modern vultures and eagles would be expected to appear. It does not follow, however, that because the living ægypiines are vulturine, the entire ancestral line was similarly adapted; even among the existing forms, *Gypaëtus* gives evidence of more rapacious tendencies. As nearly as it is possible to do so, therefore, the characters of the vultures and of the eagles should be segregated into those which are directly associated with habit, and those which are of genetic value.

There are certain skeletal features which seem to be definitely related to the vulturine habits; these characters appear in the Cathartidæ, in the Polyborinæ as contrasted with the Falconinæ, and in the Ægypiinæ as contrasted with the Aquilinæ and Buteoninæ. A list of these presumably adaptive features follows.

Vulture Types	Rapacious Types	*Neogyps errans*
1. Tarsometatarsus.	1. Tarsometatarsus.	1. Tarsometatarsus.
Middle trochlea large.	Middle trochlea smaller.	Middle trochlea small (as in rapacious types).
Internal trochlea small.	Internal trochlea large.	Internal trochlea small (as in vulture types).
Hypotarsal canal less excavated.	Hypotarsal canal more excavated.	Excavation of hypotarsal canal closer to rapacious types.
Ligamental bridge apparently absent.	Ligamental bridge present.[1]	Ligamental bridge present (as in rapacious types).

[1] This character does not apply to the Falconidæ.

Vulture Types	Rapacious Types	*Neogyps errans*
2. Tibiotarsus.	2. Tibiotarsus.	2. Tibiotarsus.
Distal end deeper anteroposteriorly.	Distal end shallow anteroposteriorly.	Distal end shallow anteroposteriorly (as in rapacious types).
Inner cnemial crest short.	Inner cnemial crest longer.	Inner cnemial crest long, but distal part diminished so that crest appears short (intermediate).
3. Femur.	3. Femur.	3. Femur.
Deep trochanteric crest.	Shallow trochanteric crest.	Shallow trochanteric crest (rapacious).
4. Pelvis.	4. Pelvis.	4. Pelvis.
Ilio-ischiatic fenestra longer anteroposteriorly.	Ilio-ischiatic fenestra shorter anteroposteriorly.	Ilio-ischiatic fenestra intermediate in length.
Fenestra extending posteriorly well beyond posterior edge of obturator foramen.	Posterior border of fenestra on line with, or only slightly posterior to obturator foramen.	Posterior extent of fenestra intermediate.
Attachment of ischium to sacrum not visible laterally through fenestra.	Attachment of ischium to sacrum visible laterally through fenestra.	Attachment of ischium to sacrum visible laterally through fenestra to the degree found in *Haliaeëtus* but less than other rapacious forms.
Posterior arch of pelvis evenly rounded.	Posterior arch of pelvis unevenly rounded with flare in ischial region.	Posterior arch of pelvis uneven with flare in ischial region (as in rapacious type).
5. Skull and mandible.—The following characters are common to the Old and New World Vultures, as compared with the eagles but are not reflected in the polyborines. However, they seem to be sufficiently related to habit to be included here.		
Toward anterior end of rostrum, tomia on line with inferior borders of external nares.	Tomia well below inferior borders of external nares throughout.	Tomia well below inferior borders of external nares (as in rapacious types).
Rami of mandible weak (high and thin).	Rami of mandible sturdy (lower and thicker).	Rami of mandible sturdy (rapacious).

With but one exception, in all of the characters related to habit listed above, we find *Neogyps* either definitely rapacious or at least intermediate. The one excepted character is the small internal trochlea of the tarsometatarsus (for digit 2).

Comparing the ægypiines vs. the eagles with the polyborines vs. the falcons, we find that though (with the exception of the skull and mandible), in the characters just listed, the polyborines parallel the ægypiines, and the falcons parallel the eagles, in other skeletal elements no parallel can be drawn. In such elements (the sternum, furcula, coracoid, scapula, humerus, ulna, radius and carpometacarpus), any differences which exist between *Polyborus* and *Falco* are of a different nature than those observed to exist between the ægypiines and the eagles. It would appear more logical, therefore, to look for true genetic relationship in these latter elements, rather than in those listed before. Among these elements all can not be given equal importance in the matter of subfamily relationship; in many of the bones, the characters vary radically within one subfamily, and can not, therefore, be given higher than generic, or even specific rank. The characters which have been found to remain constant with a subfamily are listed below.

Vultures	Eagles	*Neogyps errans*
1. Sternum.	1. Sternum.	1. Sternum.
Broad ventral manubrial spine.	Narrower ventral manubrial spine.	Broad ventral manubrial spine (as in vultures).
Low carina.	Higher carina.	Low carina (vultures).

Vultures	Eagles	*Neogyps errans*
2. Coracoid.	2. Coracoid.	2. Coracoid.
Furcular facet protruding ventrally in all but *Neophron*.	Furcular facet never protruding ventrally.	Furcular facet protruding ventrally (as in vultures).
3. Furcula.	3. Furcula.	3. Furcula.
Symphysial region not recurved dorsally.	Symphysial region recurved dorsally.	Symphysial region slightly recurved dorsally (intermediate).
Symphysis broad.	Symphysis narrower.	Symphysis broad (vultures).
4. Ulna.	4. Ulna.	4. Ulna.
Palmar side of shaft near proximal end, narrow.	Palmar side of shaft near proximal end, wider.	Palmar side of shaft near proximal end, narrow (as in vultures).
External condyle low.	External condyle high.	External condyle low (as in vultures).

In all but one of these presumably genetic characters, *Neogyps* is definitely ægypiine; in the one excepted character of the furcula, it is intermediate. These features together with still other vulturine tendencies reflected in various parts of the skeleton, as outlined in the detailed description of the separate elements, give evidence of the ægypiine origin of *Neogyps*.

Considering all the data pertaining to *Neogyps* that we have been able to set forth, it appears that this extinct Pleistocene bird was genetically related to the Old World Vultures though possessing more rapacious habits than are at present associated with that group. In the writer's opinion, this difference in habit does not warrant separating *Neogyps* from the Ægypiinæ; if this were done, it would necessitate establishing a new subfamily, since no other now existent could properly include it. Such a step seems uncalled for, and we have chosen here to maintain *Neogyps* with the Old World Vultures as originally suggested by Dr. Miller.

Neophrontops americanus Miller

Plates 26 to 29

Neophrontops americanus Miller, Univ. Calif. Publ. Bull. Dept. Geol., **9**, 106–108, figs. 1a, 1b, 1916.

Neophrontops americanus has been described from three elements, the type tarsometarsus, and the cotypes, tibiotarsus and humerus. On the basis of characters of these elements, Miller (1916, pp. 106–108) assigned the species to the family Vulturidæ (subfamily Ægypiinæ as here discussed), and called attention to its close similarity to *Neophron*. This assignment is borne out by the present study of the entire skeleton.

The species was also cited from the McKittrick Pleistocene asphalt deposits, based on the tarsometatarsus, tibiotarsus, femur, coracoid, and furcula, but none of the elements was described.

Cranium

Plate 26, figs. 1 and 1a

Material available—Six specimens in various states of fragmentation.

General characteristics—Resembling *Neophron percnopterus* or *Coragyps atratus* but recognizably distinct from the latter by reason of the absence of the basi-pterygoid processes present in cathartids.

Characters in detail—Cranium lower than *Neophron*, nearer *Coragyps*—lacking the decided rise from the supraoccipital to the "crown" which is characteristic of *Neophron percnopterus*. Cranium broader in region of temporal fossa than in *Neophron*, closer to *Coragyps*; less deeply excavated than in either. Basitemporal plate (1) flat and (2) with its posterior margin on a line with its anterior margin and the sphenoidal

rostrum; nearer *Neophron* in (1) (sides bending downward decidedly in *Coragyps*) but in (2) nearer *Coragyps* (*Neophron* with anterior margin and sphenoidal rostrum higher than posterior margin). Region of alisphenoid shallower than in *Neophron* and nearer *Coragyps*; prominent, rounded "swollen" areas present on either side of median line (on ventral side)—closest to *Haliæëtus* in this character. Facet for quadrate bounded by two small flange-like processes of about equal size; near *Neophron* in this, though posterior process slightly smaller than in *Neophron*; unlike *Coragyps*, in which the posterior process is reduced to a ridge. Shape of foramen magnum more rounded, less oval (vertically) than in *Coragyps*; nearer *Neophron*, but narrower transversely. Occipital condyle small as in *Neophron*; *Coragyps* larger. Occipital region as viewed posteriorly, broad and low as in *Neophron*; *Coragyps* narrower and higher. Supraorbital ridges as in *Neophron*, not prominent as in *Coragyps*.

Rostrum

Plate 26, figs. 2 and 2a

Material available—Six specimens.

General characteristics—Superficially resembling *Neophron percnopterus*, but stouter —wider and higher—and less extended in the posterior part.

Characters in detail—Palate flattened transversely—margins not overhanging, and maxillo-palatines close together (well apart in *Neophron*). Premaxillary curved slightly downward at anterior end as in *Neophron*; less than in any other vulture or eagle.

Measurements of Rostrum

Specimen	Breadth[1]	Height[1]	Length to external nares	Length to "maxillo-nasal" angle[2]
	mm.	*mm.*	*mm.*	*mm.*
Neophron percnopterus				
L. H. Miller				
No. 227	7.6	6.3	20.7	40.1
Neophrontops americanus				
L.A.M.				
No. J9060	12.5	8.3	21.2	30.2
F1966	13.0	8.3	21.0	30.6
F1994	13.6	8.0	19.5	30.5
J9068	16.3	8.7	23.9	30.7

[1] Measurements taken immediately anterior to external nares.

[2] See measurement "a" under Measurements of Rostrum of *Neogyps*.

Mandible

Plate 26, fig. 3

Material available—Two, left ramus.

General characteristics—Similar to *Neophron percnopterus*.

Characters in detail—Articular less prominently margined and extending farther on to the ventral side than in *Neophron*. External articular process extending upward and outward, rather than almost directly outward. Internal articular process longer than in *Neophron* and arising at a decided angle from the articular.

Sternum

Plate 26, figs. 4 and 4a

Material available—Forty-two specimens (five practically complete).

General characteristics—Resembling *Neophron percnopterus*.

Characters in detail—Carina low as in *Neophron*, and curved upward slightly at the anterior end, causing this portion to be lower than in *Neophron*; curvature not as

great as in the larger vultures, but more than in *Neophron*. Anterior carinal margin concave anteriorly; *Neophron* more nearly straight.

Ventral manubrial spine smaller than *Neophron*, the ratio of its breadth to the breadth of the ventral lip of the coracoidal sulcus varying from 12.8 to 17.0 per cent, with an average of 14.3 per cent, as compared with 18.1 per cent for *Neophron*.

Prominent flange on each side of dorsal lip of coracoidal sulcus, as in *Haliæëtus*; small protuberance in *Neophron*, slightly larger in the larger vultures, absent (only a scar) in *Aquila* and *Geranoaëtus*.

Five of the six unbroken specimens of *Neophrontops* have six true costal processes, with a small tubercle anterior to them. *Neophron* has five, and a small tubercle. The sixth specimen of *Neophrontops* also bears five.

Measurements of Sternum[1]

	a Breadth across ventral lip of sulcus	b Breadth of ventral manubrial spine	Ratio of b to a
	mm.	*mm.*	*p. ct.*
Neophron			
L. H. Miller			
No. 227.....	38.1	6.9	18.1
Neophrontops			
L.A.M.			
No. E9851...	35.7	5.2	14.5
D7588...	36.1	4.7	13.0
F2324...	37.9	5.4	14.2
C9768...	38.3	4.9	12.8
C6534...	39.3	6.7	17.0

[1] The five specimens of *Neophrontops* here listed were selected as representative from a group of eleven specimens measured.

Furcula

Plate 26, figs. 5 and 5a

Material available—One complete, nine clavicle with symphysis, four symphysis, nineteen ends.

General characteristics—Resembling *Neophron percnopterus*, but with smaller ends (shorter and narrower).

Characters in detail—Symphysis slightly more pointed than in *Neophron*, as viewed ventrally.

Furcular process diminished to a small protuberance at ventral edge as in *Neophron*, but with slight ridge extending dorsally from it on posterior side; a ridge is present in one of the available specimens of *Neophron*, but is absent in the other.

Coracoid

Plate 27, fig. 1

Material available—One hundred twelve complete specimens, sixty fragmentary.

The coracoid of *Neophrontops* is individual and can not be likened to that of any other genus. In spite of the dissimilarity to *Neophron*, these specimens are identified as *Neophrontops* by reason of (1) their relative abundance; (2) their small size; and (3) the fact that all other coracoids of the groups under consideration can be identified, leaving this group as the only one which could possibly be assigned to *Neophrontops*.

Description—Distinct posterior margin of furcular facet. Distance from sternal facet to procoracoid relatively greater than *Neophron*; ratio of this distance to length of bone averaging approximately 65.7 per cent (see Measurements of Coracoid under *Neogyps* for this ratio in compared species). *Neophrontops* of slightly larger size than *Neophron*; only one specimen out of 112 as small as *Neophron*; maximum and minimum for *Neophrontops*, 56.2 mm. and 49.5 mm., respectively; *Neophron* No. 227, 50.5 mm.

Scapula

Plate 27, figs. 2 and 2a

Material available—Eighty-one specimens.

Description—Generally similar to *Neophron percnopterus*, but without pneumatic openings on acromion; closer to *Gypaëtus* and *Neogyps* in this character.

Humerus

Plate 27, figs. 3 and 3a

Material available—Forty-two complete, fifty-nine proximal end, thirty-two distal end.

General characteristics—Similar to *Neophron percnopterus*.

Characters in detail—Proximal end: deltoid crest projecting almost at a right angle from the shaft palmad; this angle in *Neophron* is broadly obtuse. Length of crest approximately as in *Neophron*. Ligamental furrow more deeply excavated than in *Neophron*. Shaft on palmar side less flattened than in *Neophron* or other vultures; as angular as *Geranoaëtus* distal to pneumatic fossa, but flatter proximally, as in *Haliæëtus*.

Distal end flaring equally on each side of shaft as in *Neophron* and other vultures.

Curvature of shaft varying from slight curve as in *Neophron*, to more pronounced curve; never as pronounced as in *Geranoaëtus*.

Measurements of Humerus

Specimen	a Length	b Length deltoid crest	c Breadth proximal end	d Breadth distal end	Ratio b to a	Ratio c to a	Ratio d to a
	mm.	*mm.*	*mm.*	*mm.*	*p. ct.*	*p. ct.*	*p. ct.*
Neophron							
L. H. Miller							
No. 227.....	145.6	54.2	27.5	23.3	37.1	1 .8	15.9
Neophrontops							
L.A.M.							
No. G1985....	134.5	49.8	26.8	22.8	37.0	19.9	16.9
D7710...	137.2	51.7	26.6	22.4	37.6	19.3	16.3
E1945....	140.3	51.7	26.7	23.7	36.8	19.0	16.8
G1987....	141.4	50.3	25.5	22.2	35.5	18.0	15.7
E4774....	148.0	56.3	....	....	38.0	....	....

Ulna

Plate 28, figs. 1–1b

Material available—Twenty-seven complete, fifteen proximal end, forty-two distal end.

General characteristics—Similar to *Neophron percnopterus*, differing only in being shorter, with broader shaft and higher external condyle.

Measurements of Ulna

	Neophron L. H. Miller 227	Neophrontops[1]		
		E3977	D7492	D9767
	mm.	*mm.*	*mm.*	*mm.*
a Length	171.6	152.0	155.6	164.8
b Breadth of proximal end	16.2	14.8	14.8	15.6
c Breadth of distal end	9.8	9.0	9.0	9.2
d[2] Breadth of shaft at proximal end	7.3	8.1	7.2	8.5
e Breadth of shaft at middle	5.6	6.7	6.1	6.8
f[3] Height of external condyle	10.4	10.8	10.8	11.9
	p. ct.	*p. ct.*	*p. ct.*	*p. ct.*
Ratio of d to a	4.2	5.3	4.6	5.1
Ratio of f to a	6.0	7.1	6.9	7.2
Ratio of c to a	5.7	5.9	5.7	5.5
Ratio of b to a	9.4	9.7	9.5	9.4
Ratio of e to a	3.2	4.4	3.9	4.1

[1] The specimens of *Neophrontops* in this table include the maximum and the minimum in length, and the minimum in breadth of shaft.

[2] Same as measurement b in Measurements of Ulna of *Neogyps*.

[3] Same as measurement c in Measurements of Ulna of *Neogyps*.

Radius

Plate 28, figs. 2 and 2a

Material available—One complete, four proximal end, twenty-eight distal end.

General characteristics—Similar to *Neophron percnopterus*. Probably shorter, however, judging from the one complete specimen and from the length of the ulna.

Carpometacarpus

Plate 27, fig. 4

Material available—Fifty-nine complete, fifty-four complete except for metacarpal III, thirty-two with broken or worn ends.

Measurements of Carpometacarpus

Specimen	a Length	b Greatest depth proximal end	c Least depth proximal end	d Height M I	Ratio b to a	Ratio c to a	Ratio d to a
	mm.	*mm.*	*mm.*	*mm.*	*p. ct.*	*p. ct.*	*p. ct.*
Neophron L. H. Miller No. 227	77.9	18.7	16.8	11.4	24.0	21.5	14.6
Neophrontops L.A.M: No. E2069	72.9	19.0	17.1	10.3	26.0	23.4	14.1
E3558	75.0	18.4	16.6	10.2	24.5	22.1	13.5
H2477	78.5	18.4	16.7	9.7	23.4	21.2	12.3
E4423	79.0	18.9	17.4	10.4	23.9	22.0	13.1
D1175	81.6	19.1	17.2	10.3	23.4	21.0	12.6

Proximal end—Metacarpal I lower than in *Neophron*, an average of 13.1 per cent of the length as against 14.6 per cent for *Neophron*. Pisiform process heavier and more blunt than in *Neophron*.

Distal end—Distal end of metacarpal II not deeply excavated on internal side as in *Neophron*, but with only a slight furrow in this position.

Pelvis

Plate 29, figs. 1 and 1a

Material available—Twenty-six specimens, about nine of which show characteristics of pelvic bones and synsacrum clearly; other seventeen include synsacra with pelvic bones in various states of fragmentation.

General characteristics—In size and general appearance similar to *Neophron percnopterus*. The pelvis of *Coragyps atratus* is somewhat similar, but is broader and has larger, more definitely outlined openings in the shield, while the junction of ilium and ischium is broadly notched.

Characters in detail—Openings in shield even smaller than in *Neophron*. Posterior iliac crest convex rather than straight on the outer margin. There is a slight difference in the shape of the ilio-ischiatic fenestra, it being longer and narrower (more regularly oval) in shape than in *Neophron*; *Neophrontops* agrees with *Neophron* and the other vultures in the extension of the fenestra posterior to the obturator foramen, and in the fact that the ilio-sacral suture is not visible through the fenestra.

Posterior arch (see *Neogyps*) broad as in vultures, and similar to *Neophron* but for slight bending of ischium, ventral to the posterior iliac crest; this irregularity is not the same as that previously described as characterizing *Geranoaëtus* and *Aquila*, however.

Femur

Plate 29, figs. 2–2b

Material available—Fourteen complete, fifty-eight complete but for chipping and pit-wear at ends, thirty-seven fragmentary.

General characteristics—Similar to *Neophron* in general appearance, having the vulturid character of short, flaring trochanteric ridge.

Characters in detail—Head more prominent than in *Neophron*. Trochanter rising above iliac facet, forming a crest anteriorly; resembling *Sarcogyps* in this regard rather than *Neophron*. Lacking muscle tuberosity on inner side of popliteal area at distal end.

Measurements of Femur[1]

Specimen	a Length	b Breadth proximal end	c Depth proximal end	e Breadth across condyles	Ratio b to a	Ratio c to b	Ratio e to a
	mm.	*mm.*	*mm.*	*mm.*	*p. ct.*	*p. ct.*	*p. ct.*
Neophron							
L. H. Miller							
No. 227.....	70.9	14.4	13.3	14.1	20.3	92.3	19.8
Neophrontops							
L.A.M.							
No. D9192....	71.7*a*						
E1572....	79.7	14.8	15.0	13.8	18.5	101.3	17.3
E3436....	81.5	15.6	15.9	14.5	19.1	101.9	17.7
D8348....	82.7	15.7	15.7	14.3	18.9	100.0	17.2
D8950....	83.4	15.8	15.8	14.3	18.9	100.0	17.1

[1] See text figure 3 for positions of measurements.
a, approximate.

Size and proportions—Length of femur greater than in *Neophron*; minimum of *Neophrontops* 71.7 mm. as against 71.2 mm. for specimen of *Neophron* (L. H. Miller No. 227). In relative measurements, *Neophrontops* has a slightly narrower, though deeper proximal end, and is decidedly narrower across the condyles at the distal end than is *Neophron*.

TIBIOTARSUS

Plate 29, figs. 3–3b

Material available—Forty-six complete, five with both ends chipped or worn, ten proximal half, thirty-eight distal half.

General characteristics—Similar to *Neophron percnopterus* in size and general appearance, but exhibiting certain differences when considered in detail.

Characters in detail—Proximal end: breadth relative to depth and to length of bone, about as in *Neophron*, though tending to be greater. (See table.) Inner cnemial crest projecting forward more decidedly than in *Neophron*, and with a roughened distal margin. Ridge between inner and outer cnemial crests smoothly curved; this ridge in *Neophron* broken by notch just external to inner cnemial crest. Rotular crest rising gradually from proximal border as seen in internal view; thus resembling *Neophron* and differing from other vultures in which the crest rises more abruptly.

Distal end: breadth relative to length of bone, about as in *Neophron*, though tending to be smaller. Depth of distal end relative to breadth of distal end and to length of bone greater than in *Neophron*. (See table.) Internal ligamental prominence near proximal border of internal condyle; in *Neophron*, more central in position. Size of prominence varying, but tending to be smaller than in *Neophron*.

Measurements of Tibiotarsus

	Neophrontops					Neophron L. H. Miller No. 227
	L.A.M. F2094	L.A.M. F1912	L.A.M. D8176	L.A.M. E4492	L.A.M. E4489	
	mm.	*mm.*	*mm.*	*mm.*	*mm.*	*mm.*
a Length[1]	109.5	116.0	116.7	117.8	124.5	117.4
b Breadth of proximal end	13.3*a*	14.2	15.2	14.7	14.7	13.5
c Depth of proximal end	17.3*a*	17.0	18.5	18.1	18.6*a*	17.4
d Breadth of distal end	13.4	13.2	14.7	14.2	15.0	14.6
e Depth of distal end	10.2	10.7	11.3	11.3	11.2	10.6
	p. ct.	*p. ct.*	*p. ct.*	*p. ct.*	*p. ct.*	*p. ct.*
Ratio of b to a	12.1	12.2	13.0	12.4	11.8	11.5
Ratio of c to a	15.8	14.6	15.8	15.3	14.9	14.8
Ratio of b to c	76.8	83.5	82.1	81.2	79.0	77.5
Ratio of d to a	12.2	11.3	12.6	12.0	12.0	12.4
Ratio of e to a	9.3	9.2	9.7	9.6	9.0	9.2
Ratio of e to d	76.1	81.0	76.8	79.5	74.6	72.6[2]

[1] Length measured from distal condyles to proximal articular surface.
[2] This ratio 77 per cent in L.A.M. specimen of *Neophron*, No. 239.
a, approximate.

TARSOMETATARSUS

Plate 29, figs. 4 and 4a

Material available—96 complete, 72 with ends chipped or worn, 25 proximal half, 18 distal half.

General characteristics—Unmistakably ægypiine, though unlike any modern specimen in details of structure; nearest *Neophron*.

Characters in detail—Longer than *Neophron percnopterus* and with a tendency toward relatively greater slenderness of the ends and shaft (see table; also Miller's measurements [1916, p. 106]). Tubercle for tibialis anticus more nearly proximal in position than in the modern Ægypiinæ, being closer to *Coragyps atratus* in this respect. The tubercle is central in position as in *Neophron*, but does not lie in a depression as it does in that species. Calcaneal ridges more prominent and closer together than in *Neophron*, more nearly resembling *Sarcogyps calvus* in this respect, though with even closer proximity of the ridges distally than in that species.

Trochlea for digit 2 smaller relative to breadth of distal end than in *Neophron*, or any other vulture; trochleæ for digits 3 and 4 relative to distal end, the same as in *Neophron*, though actually, and in relation to the length of the bone, smaller (see table).

Measurements of Tarsometatarsus

	Neophrontops							Neophron
	L.A.M. F2004	L.A.M. E931	L.A.M. F1940	L.A.M. F1997	L.A.M. E2599	L.A.M. E3952	L.A.M. D9468	L. H. Miller No. 227
	mm.	*mm.*	*mm.*	*mm.*	*mm.*	*mm.*	*mm.*	*mm.*
a Length	85.8	85.9	89.3	92.3	93.6	96.8	97.2	81.3
b Distance from proximal end to middle of tub. for tibialis anticus	10.7	11.5	11.6	12.9	11.6	11.2	12.1	14.8
c Breadth of proximal end	14.1*a*	14.8*a*	13.8	15.4	14.0	13.9	14.2	14.7
d Breadth of distal end	14.7	14.8	15.4	16.1	14.6	14.9	....	16.8
e Depth of trochlea for digit 2	7.3	7.1*a*	7.2	7.6	6.7	6.9	....	8.7
f Depth of trochlea for digit 3	6.7	6.7	6.8	7.2	6.5	6.8	....	7.4
g Depth of trochlea for digit 4	7.6	....	7.6	8.2	7.8	7.8	....	8.5
h Breadth of shaft	....	6.7	6.4	7.0	6.6	5.2	6.3	6.5
	p. ct.	*p. ct.*	*p. ct.*	*p. ct.*	*p. ct.*	*p. ct.*	*p. ct.*	*p. ct.*
Ratio of b to a	12.4	13.3	12.9	13.9	12.3	11.5	12.4	18.2
c to a	16.4	17.2	15.5	16.6	14.9	14.3	14.6	18.0
d to a	17.1	17.2	17.2	17.4	15.5	15.3	....	20.6
h to a	....	7.7	7.1	7.6	7.0	5.3	6.4	7.6
e to d	49.6	47.9	46.7	47.2	45.8	46.3	....	51.3
f to d	45.5	45.2	44.1	44.7	44.5	45.6	....	44.0
g to d	51.7	....	49.3	50.9	53.4	52.3	....	50.1

a, approximate.

Summary

Neophrontops americanus was a small vulture, similar to the Egyptian Vulture, *Neophron percnopterus*, in general structural characters and size. Certain differences in proportions may be noted in studying the tabular summary of the sizes of the individual elements, which follows (p. 80). From this table, it appears that in the fossil bird the legs were longer, through greater length of the femoral and tarsal segments, while the wings were shortened in the region of the ulna-radius. Such differences

as exist between *Neophrontops* and *Neophron* in the physical characters of the separate elements are of less note than those which exist between *Neophron* and its contemporaries among the vultures today.

Neophrontops, with its weak bill and feet, was probably largely a carrion feeder. However, it is possible that, like *Neophron percnopterus*, it also resorted to killing small prey, such as mice, small birds, lizards, or grasshoppers. (See Brehm, 1922 p. 310, for reference to habits of *N. percnopterus*.)

Palæoborus umbrosus (Cope)

Cope (1874) originally described this species as *Cathartes umbrosus*. The type specimen, an incomplete rostrum, was taken from the Santa Fe Miocene beds of New Mexico. After the specimen had been freed of its matrix, the presence of a nasal septum was discovered, thus precluding the possibility of relationship to the Cathartidæ. Cope then (1875) transferred his species to the genus *Vultur*[1] of the Old World Vulture group.

It was Coues (1894) who finally assigned the species to a new genus, *Palæoborus*, for reasons which he stated as follows (*loc. cit.*, p. 823): "As the description and figures clearly indicate a bird generically distinct from *Cathartes*, and as the improbability of the occurrence of a true *Vultur* in North America is extreme, it is suggested that this species be made the type of a new genus, *Palæoborus*, based upon its characters given by the describer."

Most subsequent authors in referring to *Palæoborus* have included it with the Cathartidæ. In view of Cope's definite assertion that the type specimen possessed a nasal septum, such classification seems highly illogical. Possibly the reason for reassigning this species to the family from which Cope had removed it may be traced to Coues' statement regarding "the improbability of the occurrence of a true *Vultur* in North America . . . " It is probable that his reference here to *Vultur* has been interpreted to mean any member of the group to which *Vultur* belongs; it is unfortunate that he gave no summary, at that time, of the characters of the type specimen, but referred merely to the "characters given by the describer," since at the time of the original description the presence of the nasal septum was not known. It is, therefore, not surprising that later authors in listing or in briefly referring to *Palæoborus umbrosus* should have been led to place it with the Cathartidæ.[2]

Lucas (see Zittel, 1902, p. 277) had still a different idea, believing *Palæoborus* to be related to *Polyborus*.

The present writer has made a careful study of the figured specimens of *Palæoborus umbrosus* as presented by Cope (1877) and as a result, is of the opinion that this species is neither cathartid nor polyborine,[3] but belongs in the family Accipitridæ, with closest affinity to the subfamily Ægypiinæ (previously family Vulturidæ).

A description of the elements which possess the most diagnostic characters follows:

Rostrum—The characters of the rostrum, as illustrated and described by Cope (1877), which appear of significance in the matter of determining family and subfamily relationships of the species, are as follows:

(1) A nasal septum is present, thus definitely setting the species apart from the Cathartidæ. Furthermore, the beak is heavier than the cathartid beak.

[1] Now *Ægypiius*.

[2] Since writing the above, the fourth edition of the A.O.U. Checklist has included this species in the family Accipitridæ.

[3] The polyborine affinity of *Palæoborus* is also denied by Wetmore, as expressed in a statement accompanying *Palæoborus umbrosus* in the fourth edition of the A.O.U. Checklist.

(2) The external narial openings are large, thus distinguishing the species from the members of the family Falconidæ, to which *Polyborus* belongs.

(3) The anterior portions of the tomia are on a line with the inferior border of the external narial openings, as in the Ægypiinæ.

(4) There is a distinct depression, or break, between the anterior end of the nasal process of the premaxillaries and the beginning of the beak itself, as in the ægypiines; in the eagles there may be a very slight depression in this region, but the general effect is of a gradual curve from the posterior end of the nasals to the tip of the beak.

(5) The beak and mandibular symphysis are narrow as in the vultures; the mandibular symphysis is rounded ventrally with steep sides; laterally the beak and mandible together closely resemble *Sarcogyps* except for the larger external nares.

Coracoid—The anterior end is similar to *Aquila* in general characters, but the pneumatic foramina are closer to certain of the ægypiines in size and position; the bone is distinctly different from the Cathartidæ or the Polyborinæ. The ventral protrusion of the furcular facet which characterizes many of the Ægypiinæ, and is absent in all eagles, does not show in the illustration; it may be broken or absent. Though its presence would be evidence of ægypiine affinity, its absence would not indicate the contrary, since it is found in neither *Neophron* nor *Neophrontops*.

Pelvis—One vulturine character of the pelvis which can be determined from the fragment available is that of the extension of the ilio-ischiatic fenestra well posterior to the obturator foramen. The presence of distinct muscle ridges along the ventral border of the ischium distinguishes the fragment from the Cathartidæ. From this very incomplete specimen, it would be impossible to say whether the Polyborinæ or the Ægypiinæ is represented.

Femur—The femur is distinguished from both the Cathartidæ and the Falconidæ by the prominence of the proximal portion of the fibular condyle; this character would associate the fossil specimen with either the eagles or the ægypiine vultures. However, the possibility of aquiline affinity is eliminated by the presence of a short, prominent trochanteric crest. The prominence of the crest is reflected in the measurements of the proximal end; the depth of the bone through the crest, relative to the breadth of the proximal end is 81 per cent, agreeing in this ratio with *Sarcogyps calvus*. This ratio in other specimens is as follows: Ægypiinæ, 76 to 81 per cent; eagles, 63 to 75 per cent; *Neogyps*, 72 to 75 per cent; *Neophrontops*, 77 to 82 per cent; *Cathartes* and *Coragyps*, 83 per cent.

The distal end of the femur is distinguished from *Polyborus* by the absence of the protuberance proximal to the internal condyle on the posterior side.

Tibiotarsus—The tibiotarsus of *Palæoborus* is immediately set apart from the Falconidæ by the presence of a single supratendinal bridge. Its relationship to the

	External condyle	Internal condyle
	p. ct.	*p. ct.*
Palæoborus	75	80
Ægypiinæ	72 to 77	72 to 85
Eagles	62 to 69	63 to 68
Neogyps	63 to 70	68 to 73
Neophrontops	75 to 82	72 to 84
Cathartes	94	97
Coragyps	100	107

Ægypiinæ is shown in the depth of the external and internal condyles relative to the breadth of the distal end; the condyles are deeper than in the eagles and shallower than in the cathartids. The ratios are presented on page 71.

Tarsometatarsus—The shaft and general contour of the tarsometatarsus of *Palæoborus* bear resemblance to the accipitrids. The bone is broken at the distal portion of the tubercle for the tibialis anticus, so that it is impossible to determine the characters of the proximal end. However, it is obvious from the portion preserved that the shaft is considerably deeper on the external side than on the internal side, thus linking the fossil with the accipitrids and distinguishing it from either the cathartids or the polyborines. There is no suggestion of the deeply excavated, trough-like anterior surface of the shaft characteristic of the Cathartidæ. Furthermore, the contour of the bone is more curved than in either the Cathartidæ or *Polyborus*. On the posterior surface, the shaft appears to rise near the external border as in the ægypiines.

The ægypiine character of a relatively large median condyle (for digit 3) and a relatively small internal condyle (for digit 2) occurs in *Palæoborus*. The ratio of the former to the breadth of distal end is 51 per cent (equivalent to *Sarcogyps*, larger than the eagles, and smaller than the cathartids). The measurement of the internal condyle is not given by Cope, but it can be approximated from the illustration (Cope, 1877, Pl. LXVII, fig. 15b). The small size of this condyle was sufficiently noticeable for Cope to comment upon it as follows (1877, p. 294): "Of the three distal condyles, the internal has less transverse extent than the corresponding one in *A. chrysaëtos*, being but little wider than the median condyle. It terminates in the usual post-acumination." According to measurement made on the illustration its depth relative to breadth of distal end is approximately 51.5 per cent (close to *Sarcogyps*, 51.9 per cent). The ratios of depth of trochleæ to breadth of distal end follow.

	Trochlea for digit 3	Trochlea for digit 2
	p. ct.	*p. ct.*
Palæoborus	51	51.5
Ægypiinæ	44 to 51	51 to 54
Eagles	38 to 41	56 to 58
Neogyps	40 to 43	50 to 55
Neophrontops	43 to 45	49 to 53
Cathartes	55	58
Coragyps	64	57

Of all the elements described above there is none which could not be classified with the Accipitridæ or the Ægypiinæ; furthermore, in all elements which can be given a definite family or subfamily identification, the skeletal parts of *Palæoborus* may be classified with the subfamily Ægypiinæ of the family Accipitridæ.

The question has been raised as to whether all of the specimens figured and described by Cope belong to the one species. Aside from the statement made by Cope (1877, p. 295) that he found the bones lying together, "without admixture of fragments of any other animal" the present writer sees no reason to doubt that at least those elements which are described here are of one species, since no conflicting characters have been encountered. However, even the characters of the type specimen—the rostrum—alone would be sufficient to link *Palæoborus* with the Ægypiinæ more closely

than with any other raptorial group familiar to the writer. The characters of the femur, tibiotarsus and tarsometatarsus, of course, afford corroborative evidence. Though, in this instance, the coracoid is of no aid in subfamily identification, it furnishes further evidence of accipitrid affinity, while the pelvic fragment accentuates the vulturine habits of the bird, but can not definitely place it as to family. The characters of the other elements which Cope describes and figures, but which are not discussed here, do not conflict with those of the elements presented. On the other hand, however, either by reason of fragmentation or of variability which is known to exist in the element, they could contribute nothing of importance regarding the taxonomic position of the species; for this reason they have been omitted.

Conclusions Regarding the Ægypiinæ

In view of the evidence provided by *Neogyps*, *Neophrontops* and *Palæoborus*, it is reasonable to believe that the Old World Vulture group has been a part of the American avifauna from Miocene time, and has become extinct here only since the Pleistocene. Similar instances of the disappearance in America of forms once abundant here but now native only to the Old World are known among the mammals.

Whether the Pleistocene American ægypiines were descended from *Palæoborus*, or all three from a still earlier common ancestor in America, or each represents a separate migration from the Old World is a matter of speculation. *Neophrontops* is so close to *Neophron*, which is in itself a very distinct type, that it seems unlikely that these two could have developed separately over any great period of time. The writer is inclined to believe, therefore, that *Neophrontops* represents a distinct migration. An alternative possibility would be that *Neophrontops* represents the ancestral type, the migration being in the opposite direction; this alternative seems unlikely, however, since the relationship of *Neophron* to the other ægypiines of the Old World is more apparent than that of *Neophrontops* to its contemporary in North America, *Neogyps*. *Neogyps* is sufficiently removed from any modern ægypiine, by reason of its more rapacious adaptations, to lead one to suppose that it had long been separated from the Old World stock. *Palæoborus* is more vulture-like. It is a question whether a vulturine form such as *Palæoborus* could undergo the specializations fitting it for the more rapacious habits of *Neogyps*, within the space of time which elapsed between the Miocene and the Pleistocene. Unfortunately, with most of the skeleton of *Palæoborus* in a fragmentary condition, it is impossible to compare the skeletons of the two species in detail to note any possible similarities in characters other than those common to the family or subfamily. Possibly the large, more horizontally placed external nares common to both *Palæoborus* and *Neogyps* are of importance in this regard, since many of the typical modern ægypiines have the slit-like, more vertically placed openings. It should also be recalled that in certain of the adaptive characters of *Neogyps* the bird still verges on the vulturine enough to be considered intermediate rather than strictly aquiline. It is not altogether improbable, therefore, that *Palæoborus* may have been ancestral to *Neogyps*. To theorize further along this line of thought, *Palæoborus* may perhaps have been a form close to the original vulturine stock; this vulture type on encountering different environmental conditions in the Old and in the New World developed along different lines, the one leading to the true vultures of the Old World, the other to a weak-footed, semi-aquiline type (*Neogyps*), not capable of surviving in competition with the variety of true eagles with which it was contemporaneous.

SUMMARY

In the foregoing pages we have reviewed the species of eagle-like birds known from the Rancho La Brea Pleistocene, placing particular emphasis upon the presentation of the characters of the various skeletal elements of the extinct species. The two forms which are most abundantly represented in this deposit, *Aquila chrysaëtos* and *Haliæëtus leucocephalus* appear to have remained unchanged since the Pleistocene, though there is an indication of a greater range in size in each during the earlier period.

Of the extinct species, three are assigned to the subfamily Buteoninæ, one to the Aquilinæ, and two to the Ægypiinæ.

In the subfamily Buteoninæ, the fossil record of *Urubitinga* is extended into the Pleistocene; upon detailed study of characters of the species described as *Geranoaëtus fragilis* Miller, it has been deemed advisable to remove this species from the genus *Geranoaëtus* and place it with *Urubitinga*. A comparison of *U. fragilis* with specimens from the Pleistocene of Hawver Cave (previously identified as *Geranoaëtus* species), has revealed similarities between the cave form and *U. fragilis*, resulting in the assignment of the former to the genus *Urubitinga*; at the same time, the cave bird has been given the new specific name of *U. milleri*.

Unfortunately, it was possible to add almost nothing to what was already known of the skeleton of *Wetmoregyps daggetti*.[1] Certain phalanges resembling the Buteoninæ were found in three different sizes, the smallest size being most abundant, the largest size next and the medium size represented by a single specimen of each phalanx. It is thought that possibly the small bones belong with *U. fragilis*, the large with *M. woodwardi* and the medium with *Wetmoregyps*.

The elements of *Morphnus woodwardi* show resemblances to various buteonine genera and may possibly be more closely related to some genus other than *Morphnus*. Until a complete skeleton of modern *Morphnus* is available for comparison, however, the writer has maintained the species in this genus.

All three of the buteonine genera show relationship to forms now living in Central and South America. *Urubitinga*, of course, is still existent in certain southerly portions of the United States as well, and has apparently been a part of the North American avifauna as far back as the Miocene, judging from the occurrence of *U. enecta* Wetmore in the Miocene of Nebraska.

An addition has been made to the fossil representatives of the subfamily Aquilinæ, by the transferal of *Geranoaëtus grinnelli* Miller to the genus *Spizaëtus*. *S. grinnelli* has been compared with *S. ornatus* now existing in Salvador, and though of larger size than the latter species, it has been found to resemble it in general characters and proportions.

[1]See footnote on page 16 for additional information.

Several forms referred by Shufeldt to the genus *Aquila* have been reviewed and their generic allocation questioned; certain characters of *A. sodalis* and *A. pliogryps* from the Pleistocene of Oregon suggest buteonine affinity, and the writer could find nothing in either description to indicate why the two should have been described as separate species. *A. ferox* and *A. lydekkeri,* from the Eocene of Wyoming, are believed to belong to the genus of owl-like birds, *Minerva,* and possibly even to the species *M. antiqua,* since there is nothing in the descriptions to separate them.

Of the two species assigned to the Ægypiinæ, *Neophrontops* closely resembles the genus *Neophron,* now existing only in the old world. *Neogyps* also shows affinity to the Old World Vultures, though at the same time exhibiting characters indicating more rapacious habits. The characters of *Palæoborus umbrosus* Cope from the Miocene of New Mexico have been reviewed, and the ægypiine affinities of the species noted. The writer is convinced that *Palæoborus* belonged with the Ægypiinæ. The possibility of its being ancestral to the Pleistocene forms of North America is contemplated only in the case of *Neogyps; Neophrontops* so closely resembles *Neophron,* that it is believed to have been a late migrant from Old World stock. On the other hand, considering the adaptive differences between *Neogyps* and the modern ægypiines, this species must have been long separated from the old world line; the indications are, therefore, that its ancestors must have been in America at least as early as the Miocene, and it is not impossible that *Palæoborus* was in this ancestral line.

The additions of *Spizaëtus* and *Urubitinga* to the Pleistocene record are accompanied by the removal of the genus *Geranoaëtus* from the records of Rancho La Brea, Carpinteria and Hawver Cave Pleistocene. The transferal of *A. ferox* and *A. lydekkeri* to the genus *Minerva* results in the elimination of the genus *Aquila* from the Eocene record.

A list of the fossil eagle-like birds of North America, amended according to the suggestions offered in this paper is as follows:

Buteoninæ:

Geranoaëtus:
- *G. ales* Wetmore, Miocene of Nebraska
- *G. contortus* Wetmore, Miocene of Nebraska
- *G. dananus* (Marsh), Miocene of Nebraska
- *G. conterminus* Wetmore, Pliocene of Nebraska
- *Geranoaëtus* sp., Pleistocene of Florida

Buteo:
- *B. typhoius* Wetmore, Miocene of Nebraska

Urubitinga:
- *U. enecta* Wetmore, Miocene of Nebraska
- *U. fragilis* (Miller), Pleistocene of California
- *U. milleri,* new species, Pleistocene of California

Wetmoregyps daggetti (Miller), Pleistocene of California

Morphnus woodwardi Miller, Pleistocene of California

Aquilinæ:

Aquila:

Aquila sp., Miocene of Nebraska

A. (?) *pliogryps* Shufeldt, Pleistocene of Oregon

A. (?) *sodalis* Shufeldt, Pleistocene of Oregon

A. chrysaëtos (Linnæus), Pleistocene of California, Oregon and New Mexico

Spizaëtus grinnelli (Miller), Pleistocene of California

Haliæëtus leucocephalus (Linnæus), Pleistocene of California, Oregon, Nebraska, New Mexico and Florida

Ægypiinæ:

Palæoborus umbrosus (Cope), Miocene of New Mexico

Neogyps errans Miller, Pleistocene of California

Neophrontops americanus Miller, Pleistocene of California

Tables of Comparative Measurements and Proportions of Rancho La Brea Eagles and Related Modern Forms[1]

	Heterospizias meridionalis U. S. Nat. Mus. No. 227378	Geranoaëtus melanoleucus		Buteo borealis L.A.M. No. 331	Urubitinga fragilis		
		L. H. Miller No. 233	U. S. Nat. Mus. No. 18741		Max.	Mean	Min.
	mm.	*mm.*	*mm.*	*mm.*	*mm.*	*mm.*	*mm.*
Coracoid	41.1	61.3	57.3	42.0	59.5	55.1	51.9
Humerus	119.0	160.0	145.0	108.8	173.9	165.2	158.2
Ulna	138.5	189.4	166.2	128.1	201.2	189.8	182.1
Carpometacarpus	60.5	87.6	83.2	61.9	93.0	87.0	81.1
Femur	77.5	111.9	102.9	82.6	107.5	101.0	95.4
Tibiotarsus	120.2	152.9	137.1	110.0	149.6	138.8	130.4
Tarsometatarsus	104.2	114.7	105.0	85.1	113.4	105.4	96.3
Length of wing	318.0	437.0	394.4	298.8	468.1	442.0	421.4
Length of leg	301.9	379.5	345.0	277.7	370.5	345.2	322.1
	p. ct.	*p. ct.*	*p. ct.*	*p. ct.*	*p. ct.*	*p. ct.*	*p. ct.*
Ratio of humerus to ulna	85.9	84.4	87.2	84.9	86.4	87.0	86.8
Ratio of femur to humerus	65.1	69.9	70.9	75.9	61.8	61.1	62.3
Ratio of coracoid to wing	12.9	14.0	14.5	14.0	12.7	12.4	12.3
Ratio of coracoid to leg	13.6	16.1	16.6	15.1	16.0	15.9	16.1
Ratio of leg to wing	94.9	86.8	87.4	93.3	79.1	78.0	76.4

	Urubitinga urubitinga L. H. Miller No. 738	Urubitinga urubitinga D. R. Dickey No. 17185	U. anthracina anthracina D. R. Dickey No. 15618	U. anthracina subtilis D. R. Dickey No. 16950	Morphnus woodwardi		
					Max.	Mean	Min.
	mm.	*mm.*	*mm.*	*mm.*	*mm.*	*mm.*	*mm.*
Coracoid	45.1	44.7	41.3	39.2	73.2	69.5	67.7
Humerus	120.8	119.1	109.5	105.3	217.5[2]	206.3[2]	193.1[2]
Ulna	138.6	137.8	126.6	123.7	257.7[2]	240.4[2]	223.1[2]
Carpometacarpus	61.5	59.2	58.4	56.0	128.4	116.3	104.4
Femur	88.5	84.2	74.9	71.8	130.7	126.5	124.6
Tibiotarsus	144.2	138.8	108.0	104.1	190.8	177.7	171.4
Tarsometatarsus	119.5	115.3	88.3	83.3	140.6	131.5	125.0
Length of wing	320.9	316.1	294.5	285.0	603.6	563.0	520.6
Length of leg	352.2	338.3	271.2	259.2	462.1	435.7	420.6
	p. ct.	*p. ct.*	*p. ct.*	*p. ct.*	*p. ct.*	*p. ct.*	*p. ct.*
Ratio of humerus to ulna	87.1	86.4	86.4	85.1	84.3	85.8	86.5
Ratio of femur to humerus	73.2	70.6	68.4	68.1	60.0	61.3	64.3
Ratio of coracoid to wing	14.0	14.1	14.1	13.7	12.1	12.3	13.0
Ratio of coracoid to leg	12.8	13.2	15.3	15.1	15.8	15.9	16.0
Ratio of leg to wing	109.7	107.0	92.0	90.9	76.5	77.3	80.0

[1] The fossil species being represented entirely by unassociated elements, the lengths of leg and of wing, as well as the proportions have been derived by a correlation of maximum with maximum and minimum with minimum. It is, of course, understood that the results so obtained can not exactly parallel the proportions obtained from a correlation of the associated elements of one individual, but can merely afford a general idea of the relationship of elements in the fossil forms.

[2] The measurements of ulna and humerus have been estimated from broken bones, since no complete specimens of these elements were available. Consequently, the length of wing, as well as all ratios involving the ulna, humerus, or entire wing should be considered as tentative estimates.

TABLES OF COMPARATIVE MEASUREMENTS AND PROPORTIONS OF RANCHO LA BREA EAGLES AND RELATED MODERN FORMS
(*Continued*)

Element	Aquila chrysaëtos Rancho La Brea		Aquila chrysaëtos Recent				Spizaëtus ornatus		Spizaëtus grinnelli	
	Max.	Min.	M.V.Z. No. 42686	L. H. Miller No. 927	L. H. Miller No. 923	M.V.Z. No. 41410	D. R. Dickey No. 16929	D. R. Dickey No. 16872	Max.	Min.
	mm.	*mm.*	*mm.*	*mm.*	*mm.*	*mm.*	*mm.*	*mm.*	*mm.*	*mm.*
Coracoid	76.8	61.2	.....	69.5	62.9	62.4	48.6	.....	63.3	52.3
Humerus	216.0	173.7	194.0	192.7	178.8	171.9	.....	116.0	173.1	142.0
Ulna	244.1	211.9	225.6[1]	224.9	210.1	.....	.....	.....	200.6	165.5
Carpometacarpus	112.9	92.5	105.5	104.5	96.6	.....	.....	.....	97.0	72.6
Femur	135.8	114.0	.....	129.2	122.6	118.6	93.6	91.8	121.3	112.6
Tibiotarsus	172.8	148.0	.....	165.1	160.2	153.2	132.0	127.0	164.6	150.1
Tarsometatarsus	107.6	90.7	116.8	101.8	98.7	94.3	96.8	92.0	114.8	100.6
Length of wing	572.9	478.1	525.1	522.1	485.5	.....	.....	.....	470.7	380.1
Length of leg	416.2	352.7	.....	396.1	381.5	366.1	322.4	310.8	400.7	363.3
	p. ct.	*p. ct.*	*p. ct.*	*p. ct.*	*p. ct.*	*p. ct.*	*p. ct.*	*p. ct.*	*p. ct.*	*p. ct.*
Ratio of humerus to ulna	88.4	81.9	85.8	85.6	85.1	.....	.....	.....	86.2	85.8
Ratio of femur to humerus	62.8	64.4	.....	67.0	68.5	68.9	.....	79.1	70.0	79.2
Ratio of coracoid to wing	13.4	12.8	.....	13.3	12.9	.....	.....	.....	13.4	13.7
Ratio of coracoid to leg	18.4	17.3	.....	17.5	16.4	17.0	15.0	.....	15.7	14.3
Ratio of leg to wing	72.6	73.7	.....	75.8	78.5	.....	.....	.....	85.1	95.5

[1] M.V.Z. No. 50475 measures 227.0 mm.

TABLES OF COMPARATIVE MEASUREMENTS AND PROPORTIONS OF RANCHO LA BREA EAGLES AND RELATED MODERN FORMS (*Continued*)

Element	Haliæëtus leucocephalus					
	Rancho La Brea		Recent			
	Max.	Min.	MVZ. No. 8326[1]	L.A.M. No. 291[1]	D. R. Dickey No. 22944[2]	L. H. Miller No. 626[2]
	mm.	*mm.*	*mm.*	*mm.*	*mm.*	*mm.*
Coracoid	83.7	68.5	80.2	.....	74.6	69.1
Humerus	243.0	204.0	226.5	228.0	213.5	196.5
Ulna	279.5	240.0	250.0	264.1	246.5	.....
Carpometacarpus	128.3	103.6*a*	115.1	119.7	107.4	.....
Femur	129.2	111.8	126.0	125.8	121.8	112.2
Tibiotarsus	174.0	150.0	168.5	166.5	157.0	.....
Tarsometatarsus	103.3	84.7	97.6	97.1	93.8	87.9
Length of wing	650.8	547.6	591.6	611.8	567.4	.....
Length of leg	406.5	346.5	391.7	389.4	372.6	.....
	p. ct.	*p. ct.*	*p. ct.*	*p. ct.*	*p. ct.*	*p. ct.*
Ratio of humerus to ulna	87.0	85.0	90.6	86.1	86.5	.....
Ratio of femur to humerus	53.2	54.6	55.6	55.1	56.8	57.1
Ratio of coracoid to wing	12.8	12.5	13.5	....	13.1	.....
Ratio of coracoid to leg	20.5	19.7	20.4	....	19.9	.....
Ratio of leg to wing	62.4	63.4	66.2	64.6	65.7	.....

[1] *Haliæëtus l. alascanus.* [2] *Haliæëtus l. leucocephalus.* *a*, approximate.

Element	Neogyps errans			Gypaëtus barbatus L. H. Miller No. 263	Sarcogyps calvus L.A.M. No. 226	Ægypiinæ, species? L.A.M. No. 232
	Max.	Mean	Min.			
	mm.	*mm.*	*mm.*	*mm.*	*mm.*	*mm.*
Coracoid	65.9	67.7	69.9	88.3	77.8	73.8
Humerus	217.6	210.2	199.0	241.9	212.4	199.8
Ulna	251.7	243.8	236.0	275.0	274.9	280.2
Carpometacarpus	111.5	105.8	98.4	122.8	107.6	106.3
Femur	113.4	108.4	103.4	125.0	112.4	104.3
Tibiotarsus	153.6	147.2	140.9	170.9	158.9	159.4
Tarsometatarsus	93.0	88.5	84.0	99.5	95.5	108.4
Length of wing	580.8	558.9	537.2	639.5	594.9	586.3
Length of leg	360.0	344.1	328.3	395.4	366.8	372.1
	p. ct.	*p. ct.*	*p. ct.*	*p. ct.*	*p. ct.*	*p. ct.*
Ratio of humerus to ulna	86.4	86.1	85.9	87.9	77.2	71.3
Ratio of femur to humerus	52.1	51.5	50.9	51.6	52.9	52.2
Ratio of coracoid to wing	12.0	12.1	12.2	13.2	13.0	12.5
Ratio of coracoid to leg	19.4	19.7	20.0	22.3	21.2	19.8
Ratio of leg to wing	62.1	61.5	61.6	60.2	61.6	63.4

TABLES OF COMPARATIVE MEASUREMENTS AND PROPORTIONS OF RANCHO LA BREA EAGLES AND RELATED MODERN FORMS (*Continued*)

Element	Number of specimens of Neophrontops	Number larger than Neophron	Number smaller than Neophron	Neophrontops			Neophron
				Max.	Mean	Min.	
				mm.	*mm.*	*mm.*	*mm.*
Beak							
Length	4	0	4	30.7	30.5	30.2	40.1
Breadth	4	4	0	16.3	13.8	12.5	7.6
Sternum							
Breadth of ventral lip of sulcus	11	4	7	39.3	37.5	35.7	38.1
Coracoid[1]	112	111	1	56.2	52.8	49.5	50.5
Humerus[1]	42	8	34	148.0	141.2	134.5	145.6
Ulna[1]	27	0	27	164.8	158.4	152.0	171.6
Carpometacarpus[1]	113	50	63	81.6	77.2	72.9	77.9
Femur[1]	72	72	0	83.4	77.5	71.7	71.2
Tibiotarsus[1]	46	20	26	124.5	117.0	109.5	117.4
Tarsometatarsus[1]	167	167	0	97.2	91.5	85.8	81.3
Length of wing	..	..	..	394.4	376.8	359.4	407.5
Length of leg	..	..	..	305.1	286.0	267.0	269.7
				p. ct.	*p. ct.*	*p. ct.*	*p. ct.*
Ratio of humerus to ulna	..	..	..	89.1	89.1	88.4	79.1
Ratio of femur to humerus	..	..	..	56.3	54.8	53.3	48.9
Ratio of coracoid to wing	..	..	..	14.2	14.0	13.7	12.3
Ratio of coracoid to leg	..	..	..	18.4	18.4	18.5	18.7
Ratio of leg to wing	..	..	..	77.3	75.9	74.2	66.1

[1] Measurement of length.

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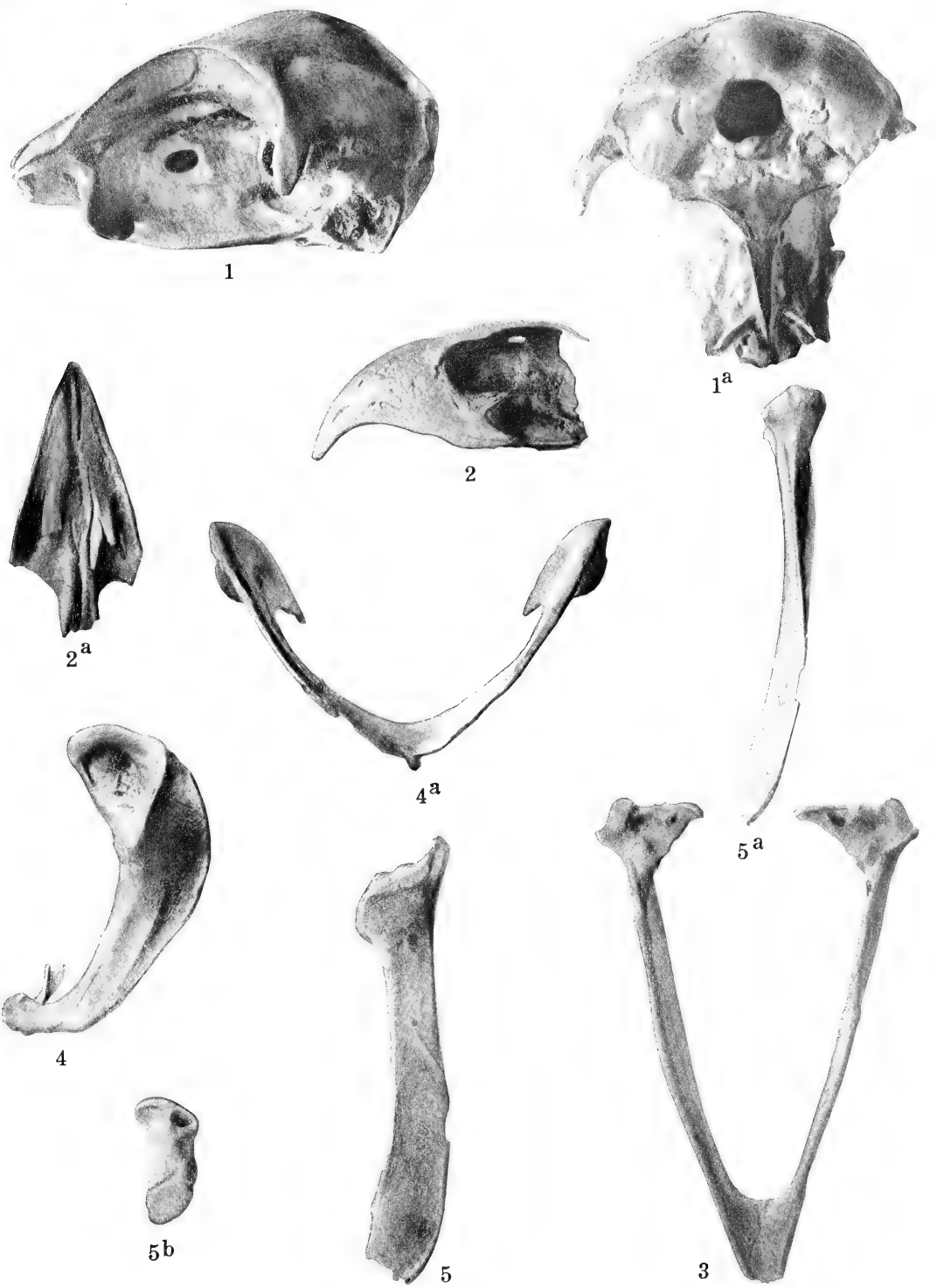
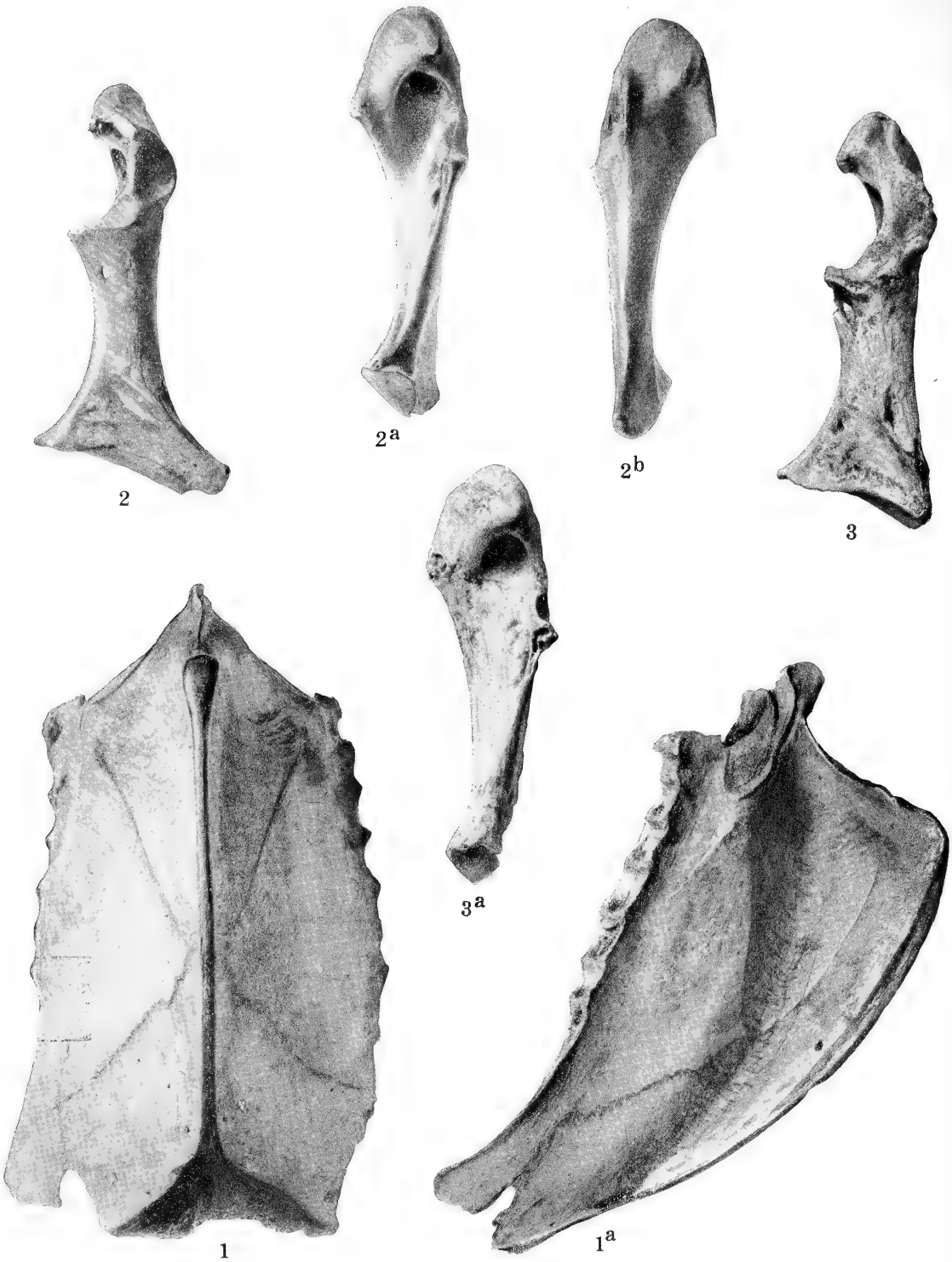


Urubitinga fragilis (Miller). Los Angeles Museum Collections.

FIGS. 1 and 1a. Cranium, No. D1184, lateral and posteroventral views, × 1.
2 and 2a. Rostrum, No. D1142, lateral and ventral views, × 1.
3. Mandible, No. D2029, dorsal view, × 1.
4 and 4a. Furcula, No. C8184, lateral and anterior views, × 1.
5, 5a and 5b. Scapula, No. C5485, ventral, internal and anterior views, × 1.

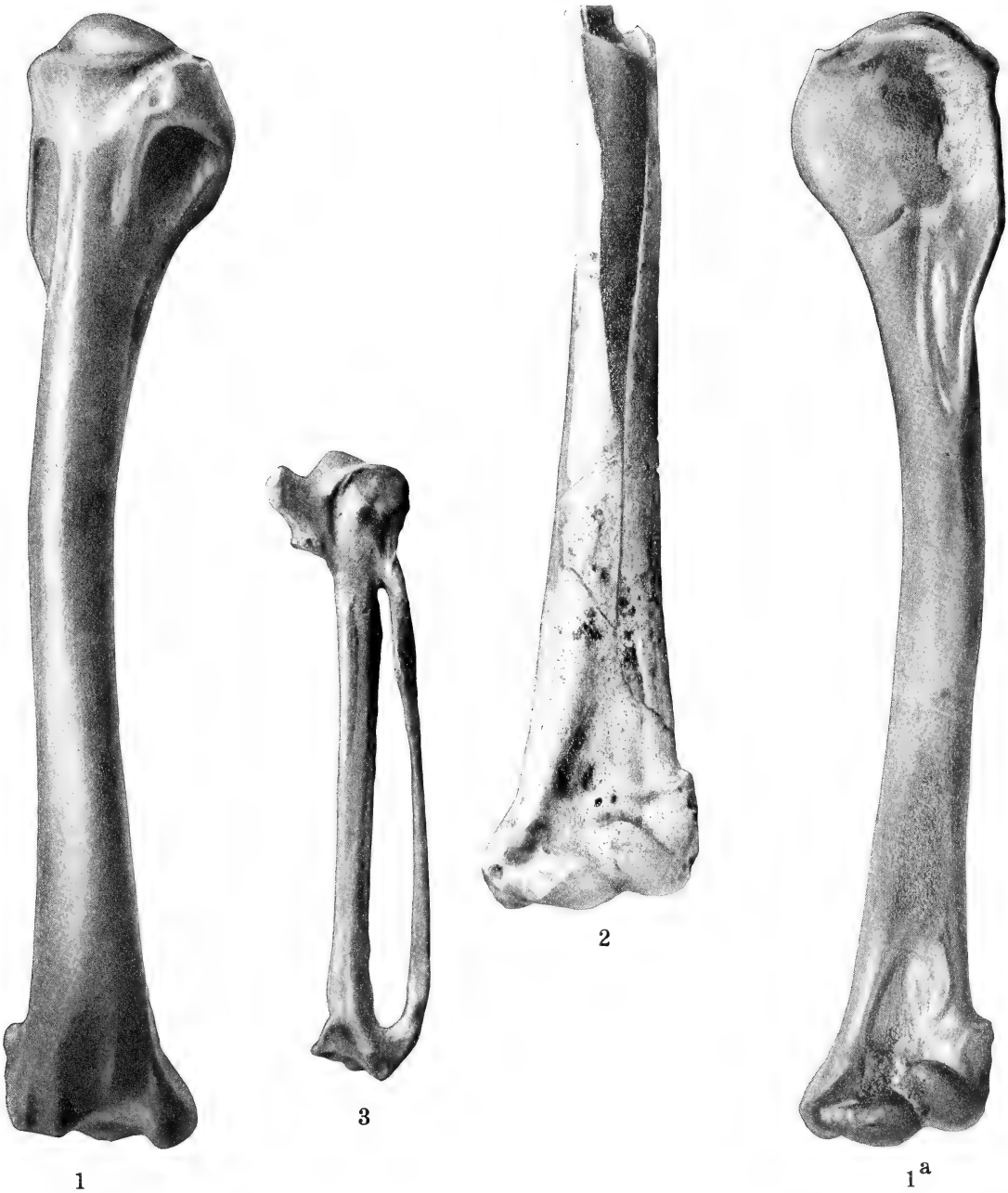


Urubitinga fragilis (Miller). Los Angeles Museum Collections.

FIGS. 1 and 1a. Sternum, No. C7929, ventral and lateral views, × 1.
2, 2a and 2b. Coracoid, No. E4079, dorsal, internal and external views, × 1.

Urubitinga milleri, new species. University of California Collections.

3 and 3a. Coracoid, No. 11050, dorsal and internal views, × 1.
Type specimen. Hawver Cave.



Urubitinga fragilis (Miller). Los Angeles Museum Collections.

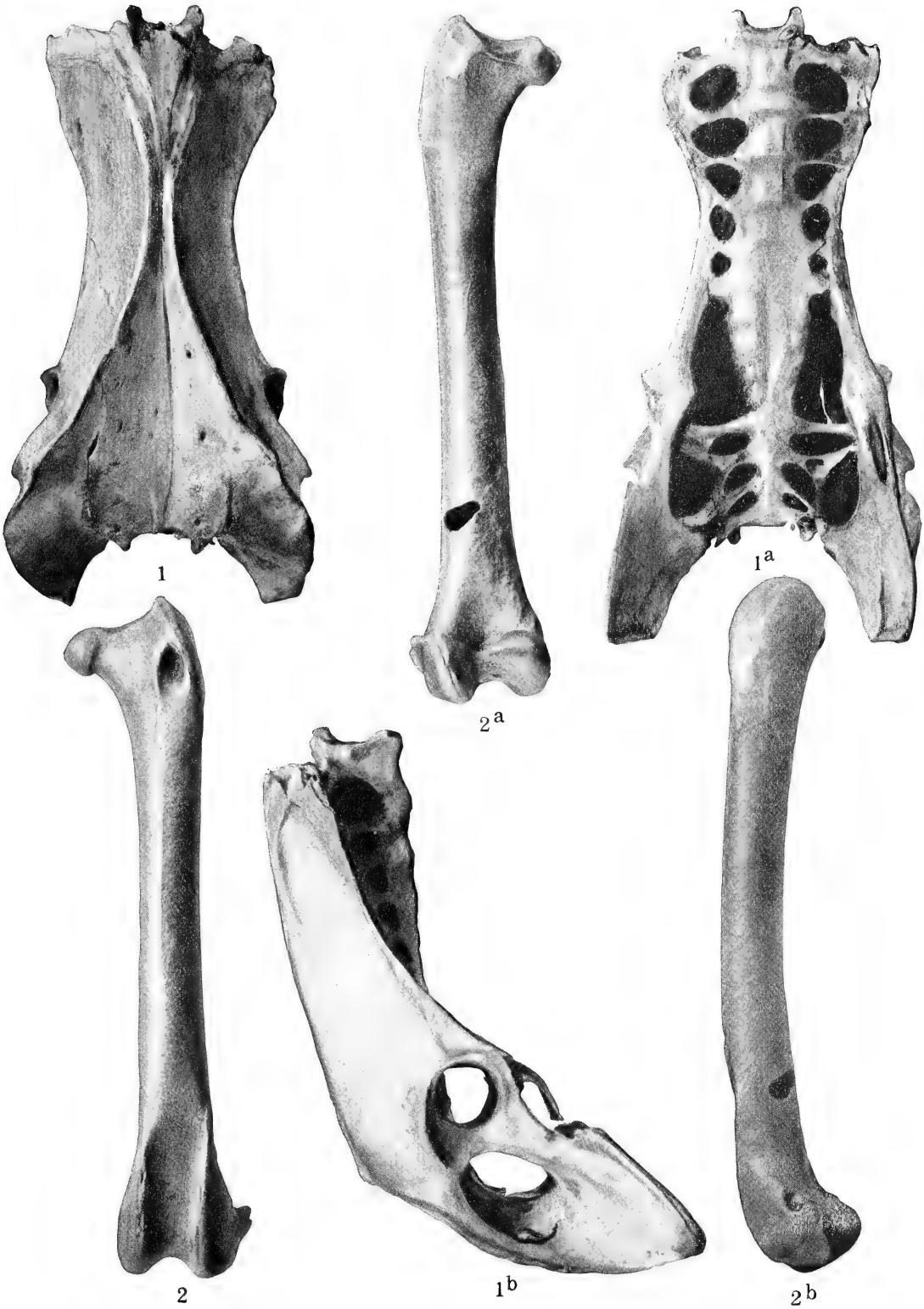
FIGS. 1 and 1a. Humerus, No. C8735, anconal and palmar views, × 1.
3. Carpometacarpus, No. E1091, internal view, × 1.

Urubitinga milleri, new species. University of California Collections.

2. Distal end of humerus, No. 11015, palmar view, × 1. Hawver Cave.

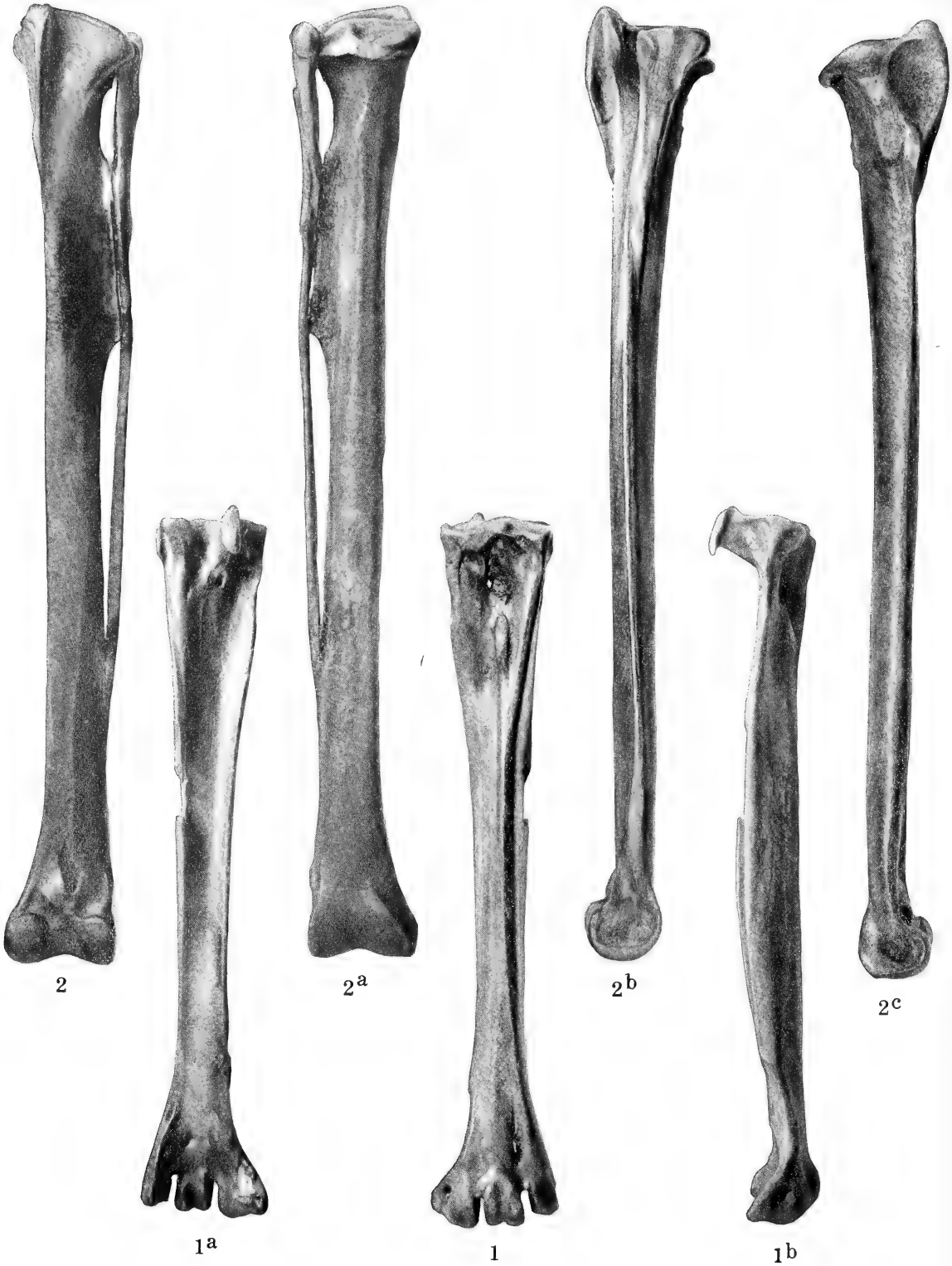
Urubitinga fragilis (Miller). Los Angeles Museum Collections.

FIGS. 1, 1a and 1b. Ulna, No. C5261, palmar, external and internal views, × 1.
2 and 2a. Radius, No. D8354, anconal and external views, × 1.



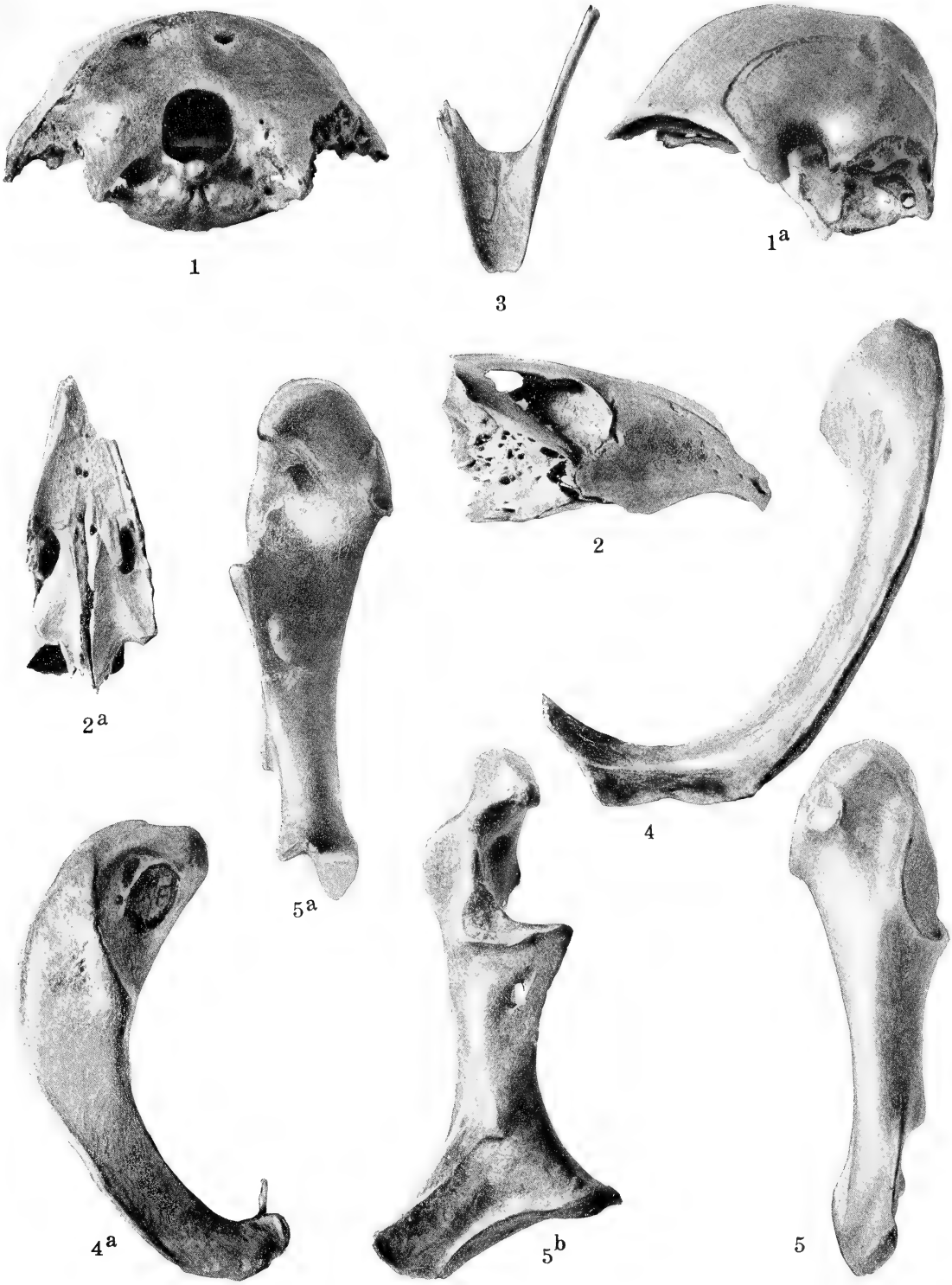
Urubitinga fragilis (Miller). Los Angeles Museum Collections.

FIGS. 1, 1a and 1b. Pelvis, No. C6481, dorsal, ventral and lateral views, × 1.
2, 2a and 2b. Femur, No. C684, anterior, posterior and external views, × 1.



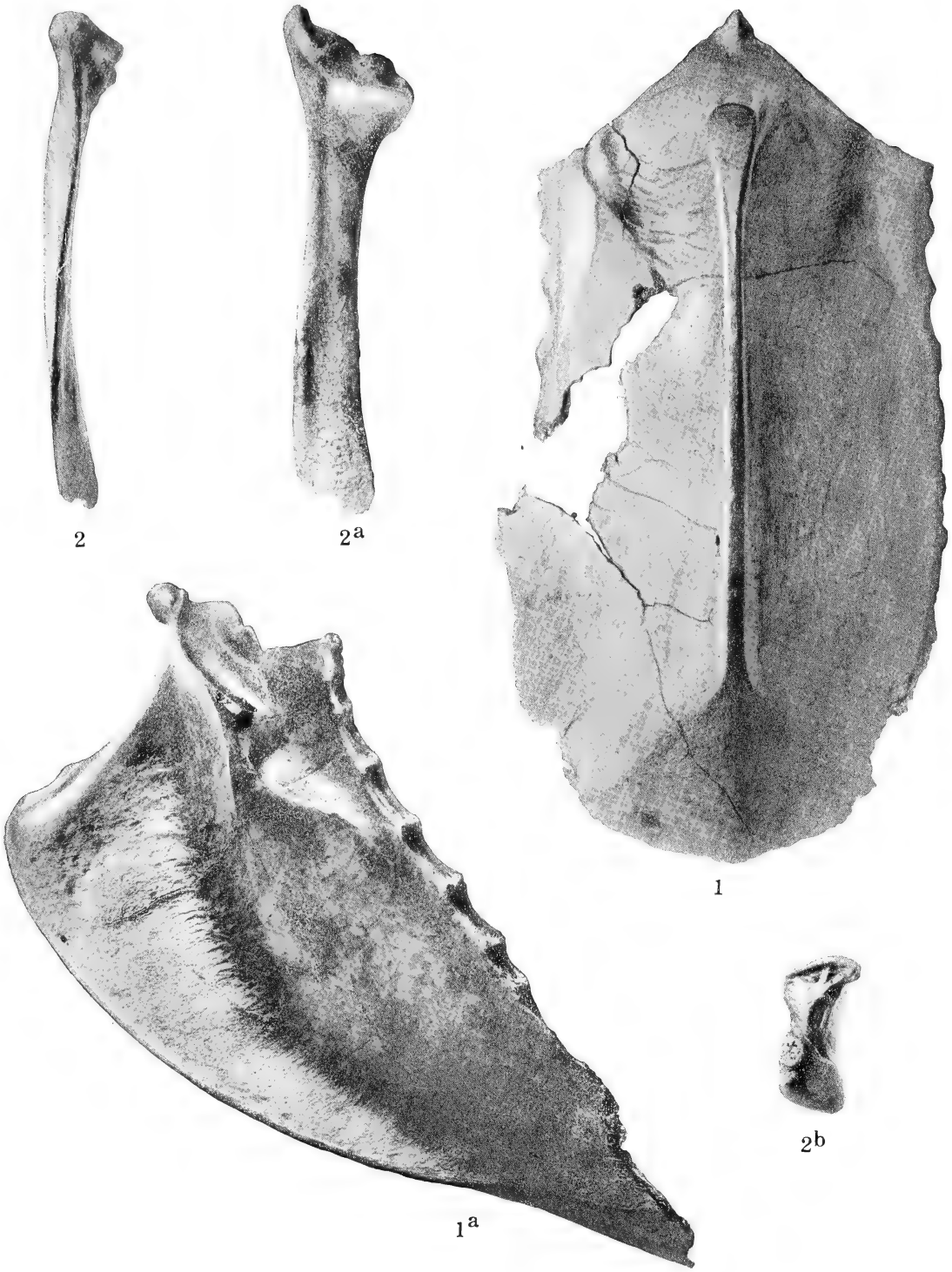
Urubitinga fragilis (Miller). Los Angeles Museum Collections.

FIGS. 1, 1a and 1b. Tarsometatarsus, No. E893, anterior, posterior and lateral views, × 1.
2, 2a, 2b and 2c. Tibiotarsus, No. C7332, anterior, posterior, external and internal views, × 1.



Morphnus woodwardi Miller. Los Angeles Museum Collections.

FIGS. 1 and 1a. Cranium, No. F3172, posterior and lateral views, × 1.
2 and 2a. Rostrum, No. C6846, lateral and ventral views, × 1.
3. Symphysis of mandible, No. D1019, dorsal view, × 1.
4 and 4a. Furcula, No. D3056, anterior and lateral views, × 1.
5, 5a and 5b. Coracoid, No. D4676, external, internal and dorsal views, × 1.

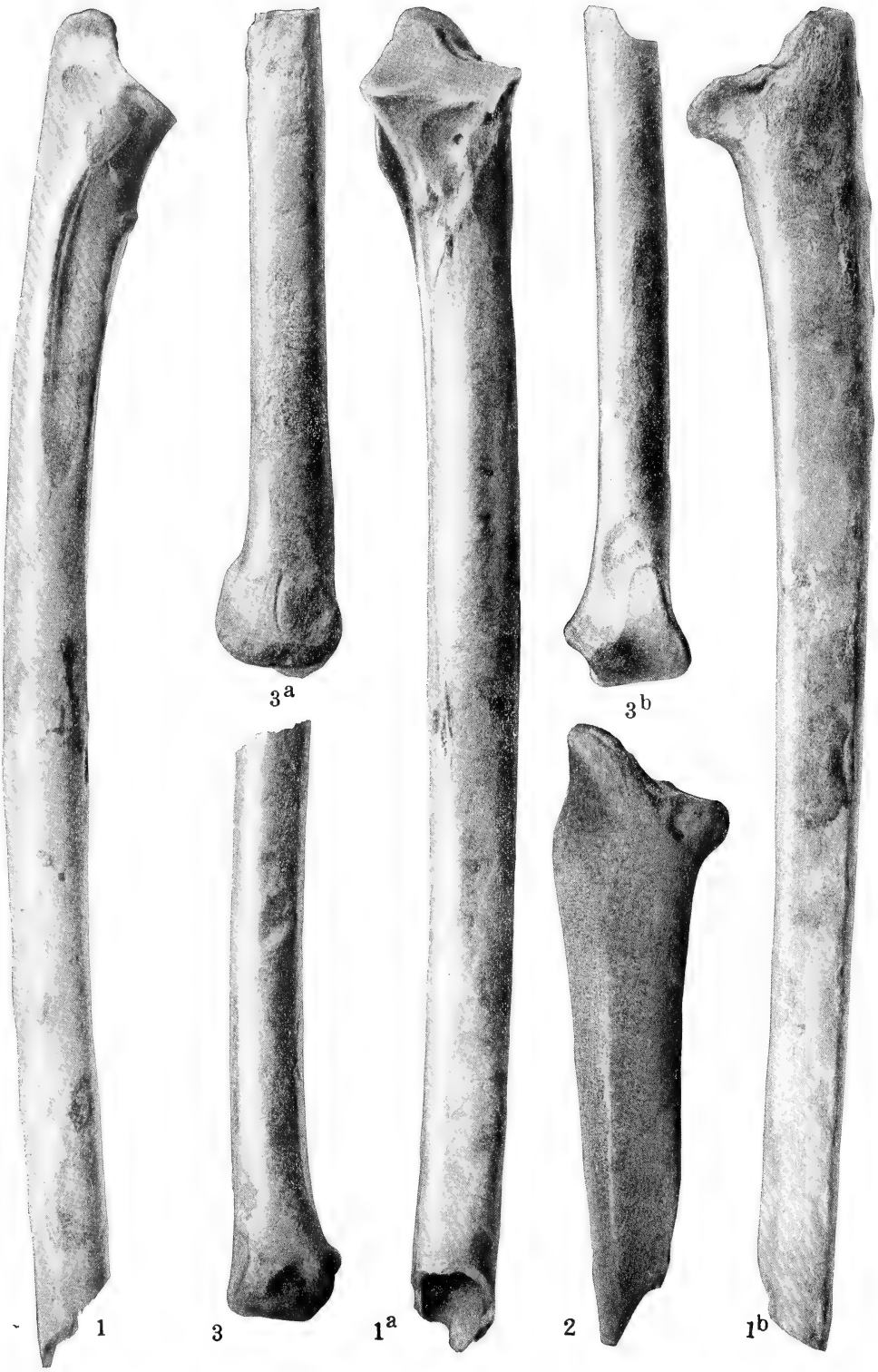


Morphnus woodwardi Miller. Los Angeles Museum Collections.

FIGS. 1 and 1a. Sternum, No. D2398, ventral and lateral views, × 1.
2, 2a and 2b. Scapula, No. D4816, internal, ventral and anterior views, × 1.

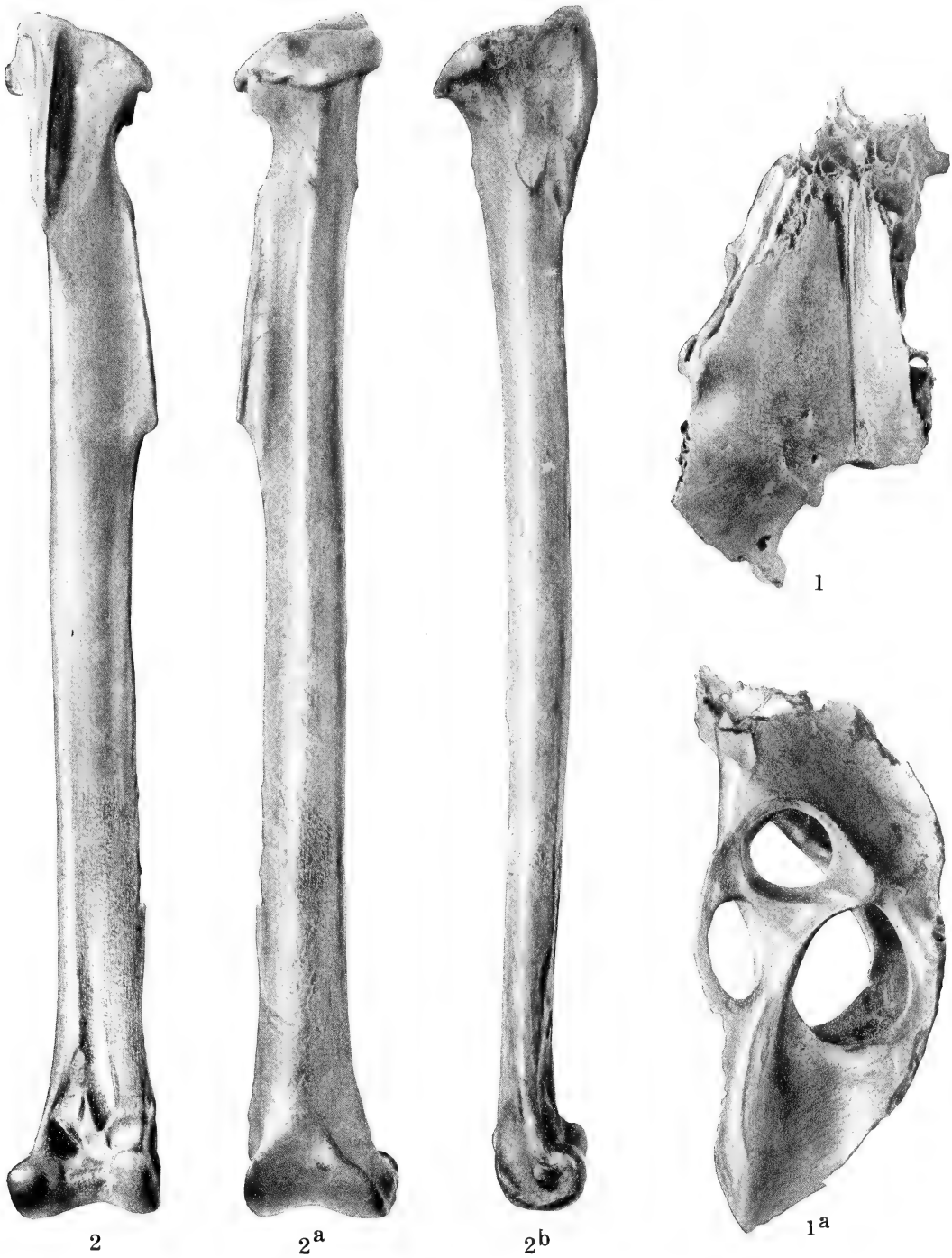
Morphnus woodwardi Miller. Los Angeles Museum Collections.

FIGS. 1 and 1a. Humerus, No. D6743, palmar and anconal views, × 1.
2. Proximal end of radius, No. C4224, anconal view, × 1.
3. Carpometacarpus, No. D1702, internal view, × 1.



Morphnus woodwardi Miller. Los Angeles Museum Collections.

FIGS. 1, 1a, 1b. Proximal end ulna, No. C9264, internal, palmar and external views, × 1.
2. Proximal end of ulna, No. G7554, anconal view, × 1.
3, 3a, 3b. Distal end ulna, No. D5177, palmar, external and internal views, × 1.

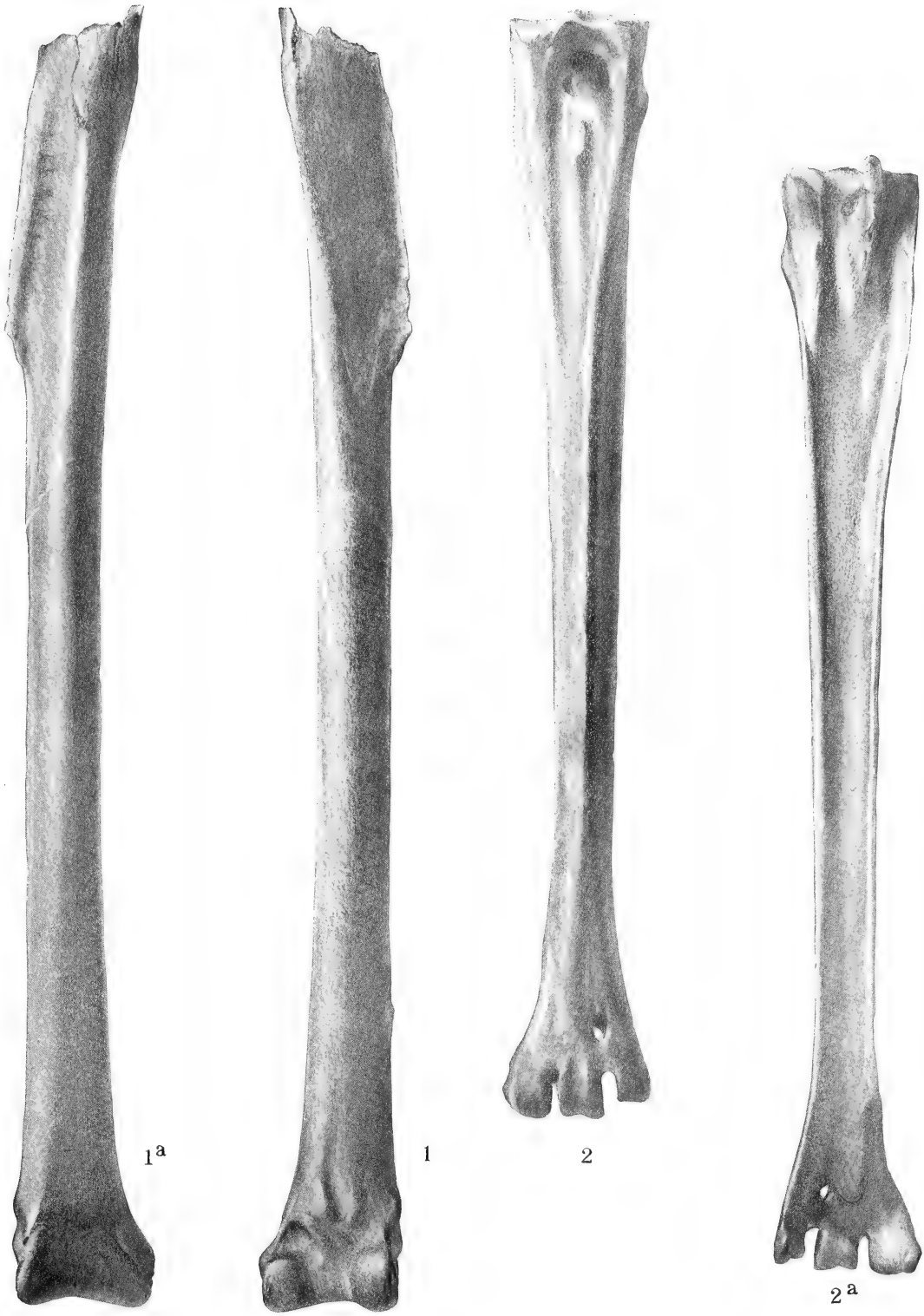


Morphnus woodwardi Miller. Los Angeles Museum Collections.

FIGS. 1 and 1a. Posterior portion of pelvis, No. C8858, dorsal and lateral views, × 1.
2, 2a and 2b. Tibiotarsus, No. D1974, anterior, posterior and internal views, × 1.

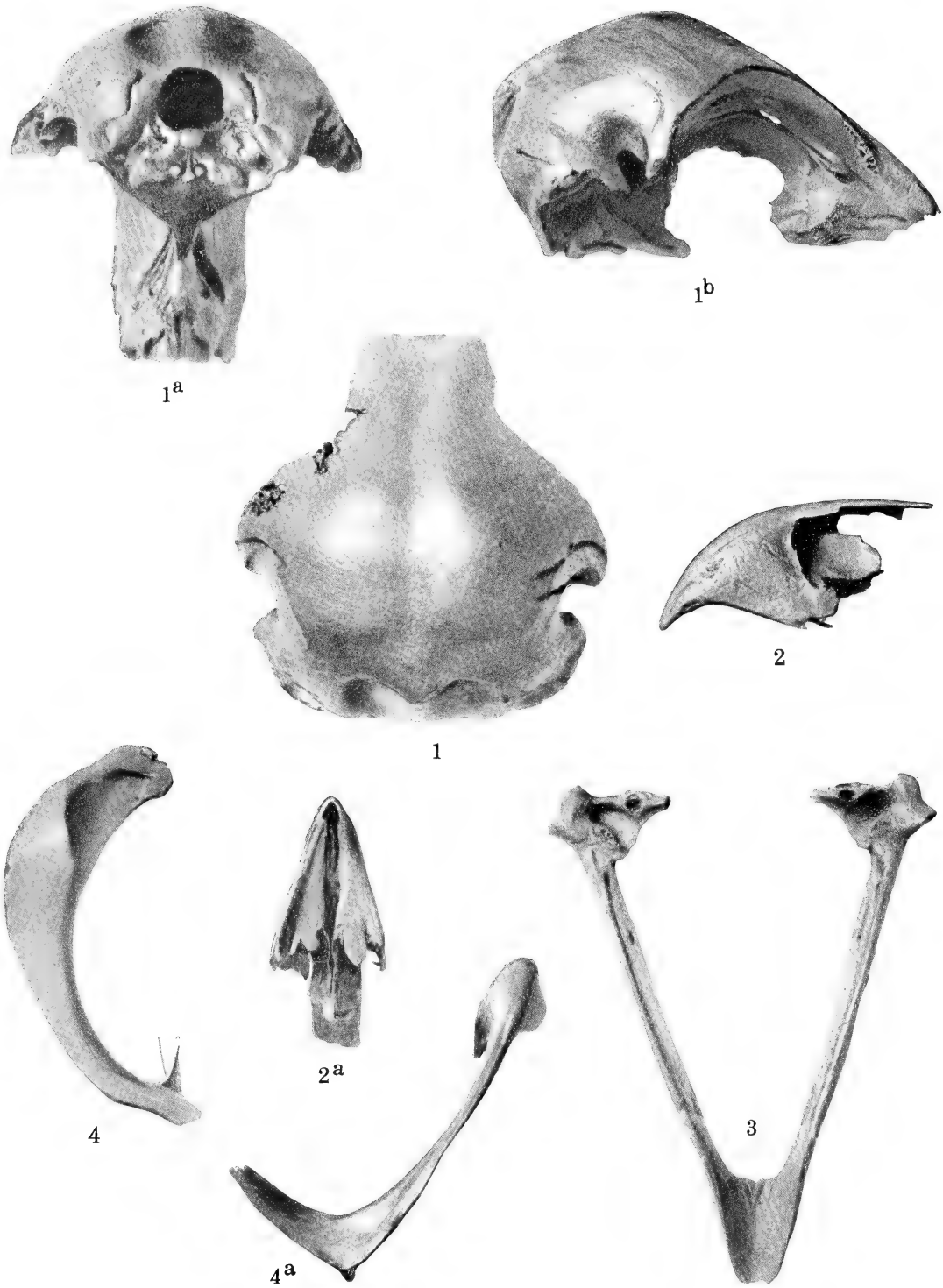
Morphnus woodwardi Miller. Los Angeles Museum Collections.

FIGS. 1, 1a and 1b. Femur, No. C1111, anterior, posterior and external views, × 1.
2, 2a and 2b. Tarsometatarsus, No. C6644, anterior, posterior and internal views, × 1.



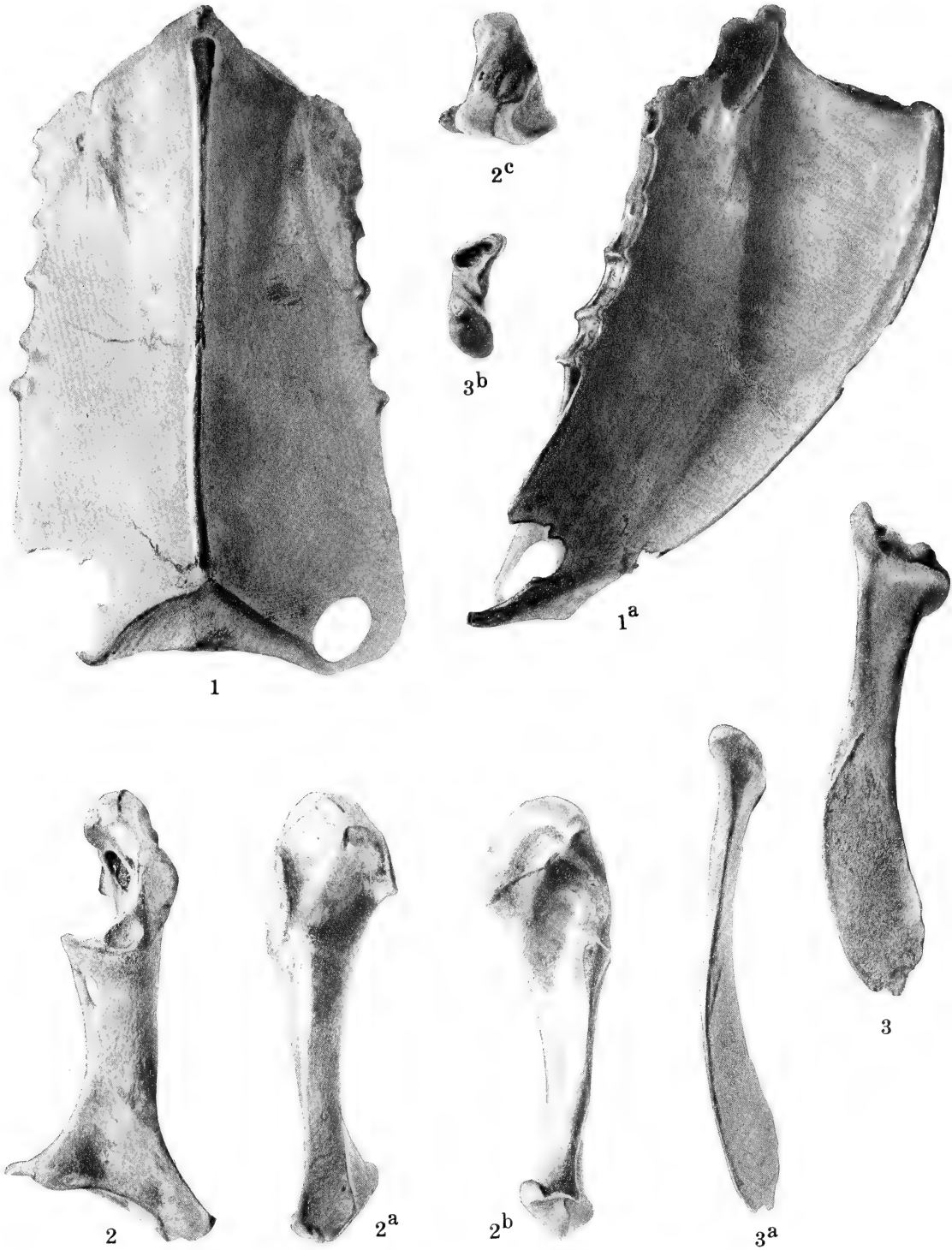
Wetmoregyps daggetti (Miller). Los Angeles Museum Collections.

FIGS. 1 and 1a. Tibiotarsus, No. J9744, anterior and posterior views, × 1.
2 and 2a. Tarsometatarsus, No. K3159, anterior and posterior views, × 1.



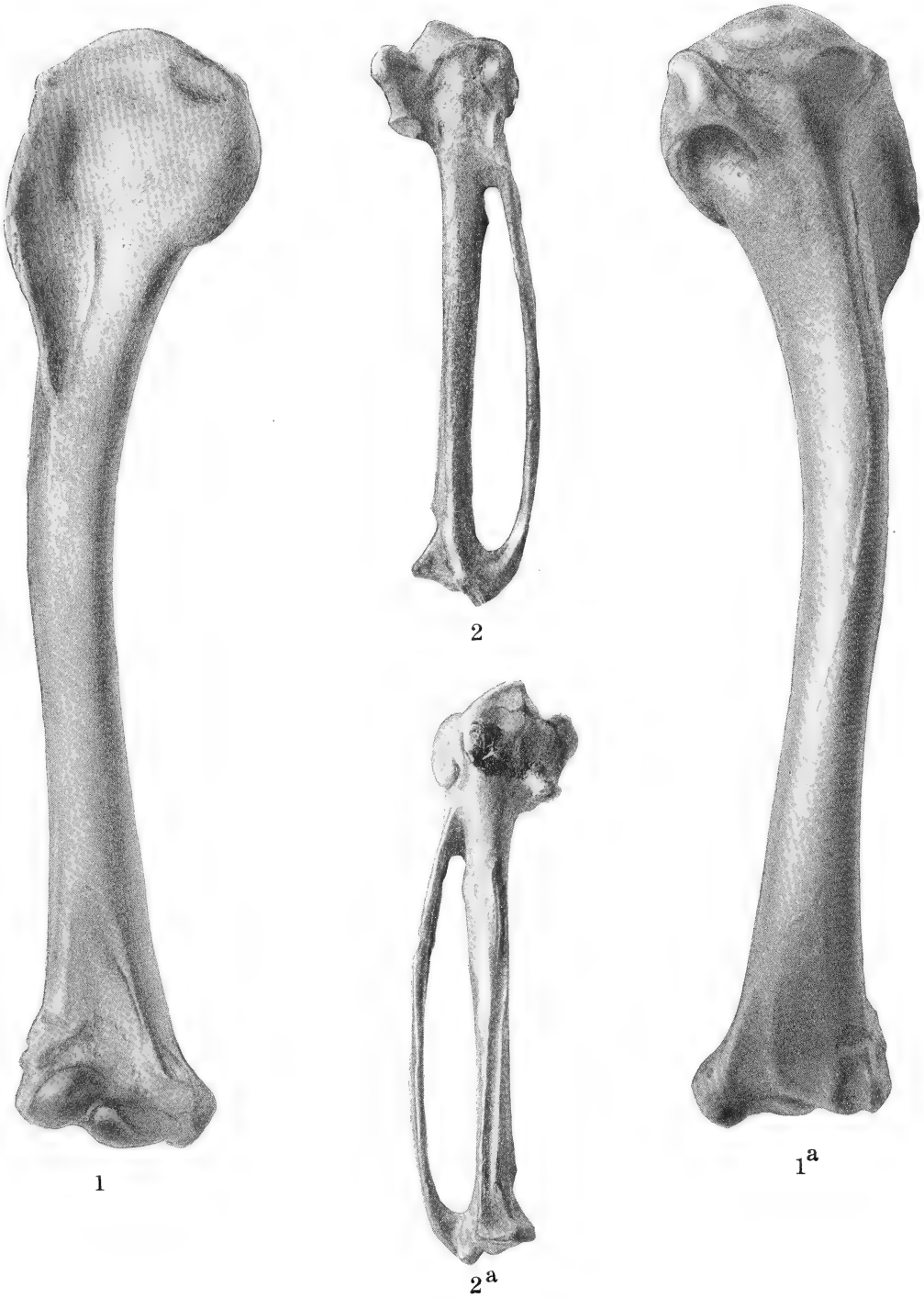
Spizaëtus grinnelli (Miller). Los Angeles Museum Collections.

FIGS. 1. Cranium, No. E3600, dorsal view, × 1.
1a and 1b. Cranium, No. D4284, posteroventral and lateral views, × 1.
2 and 2a. Rostrum, No. F3071, lateral and ventral views, × 1.
3. Mandible, No. C5852, dorsal view.
4 and 4a. Furcula, No. C2508, lateral and anterior views, × 1.



Spizaëtus grinnelli (Miller). Los Angeles Museum Collections.

FIGS. 1 and 1a. Sternum, No. D5981, ventral and lateral views, × 1.
2, 2a, 2b and 2c. Coracoid, No. C5842, dorsal, external, internal, anterior views, × 1.
3, 3a and 3b. Scapula, No. C4450, ventral, internal and anterior views, × 1.

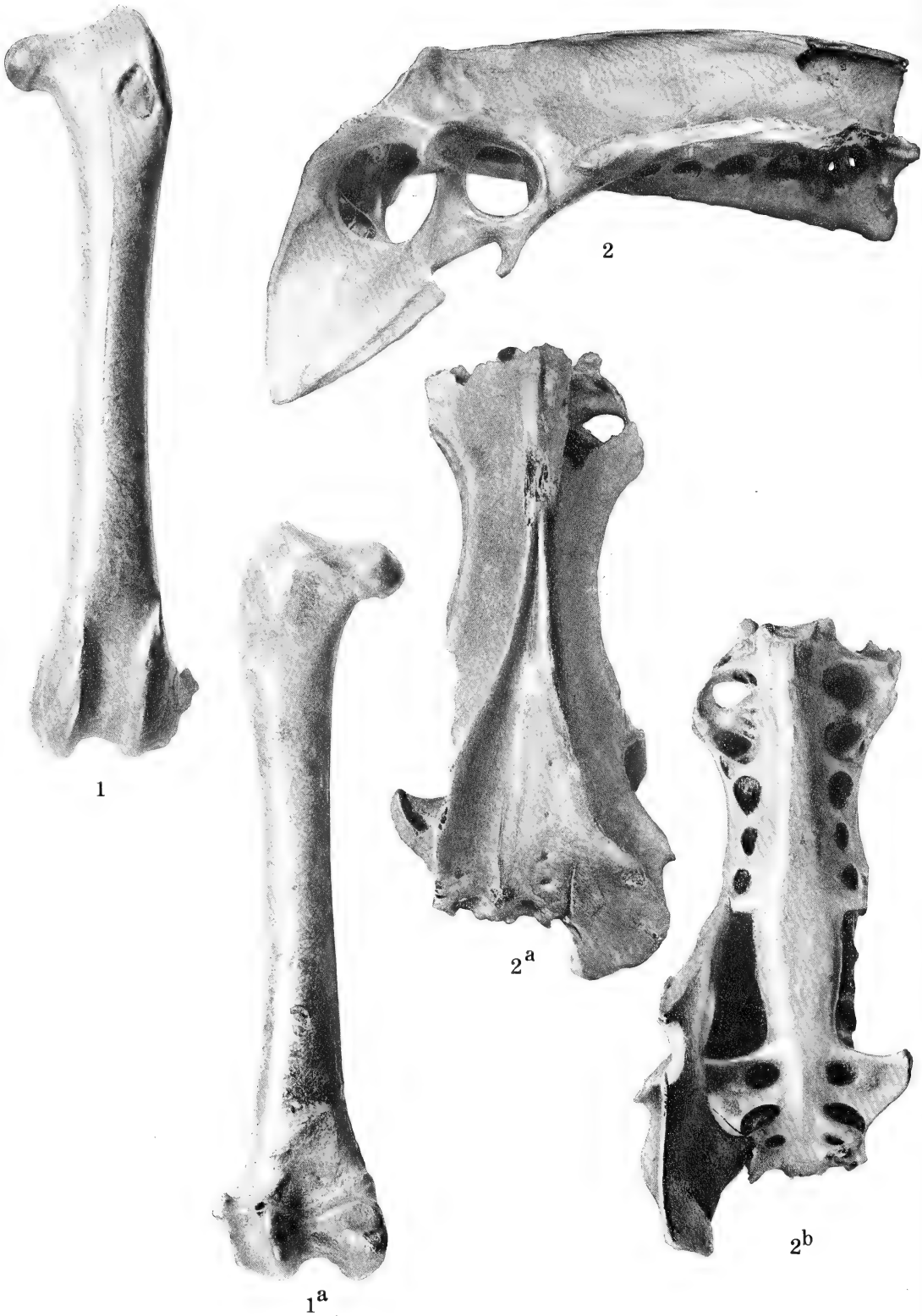


Spizaëtus grinnelli (Miller). Los Angeles Museum Collections.

FIGS. 1 and 1a. Humerus, No. D2365, palmar and anconal views, × 1.
2 and 2a. Carpometacarpus, No. C1587, internal and external views, × 1.

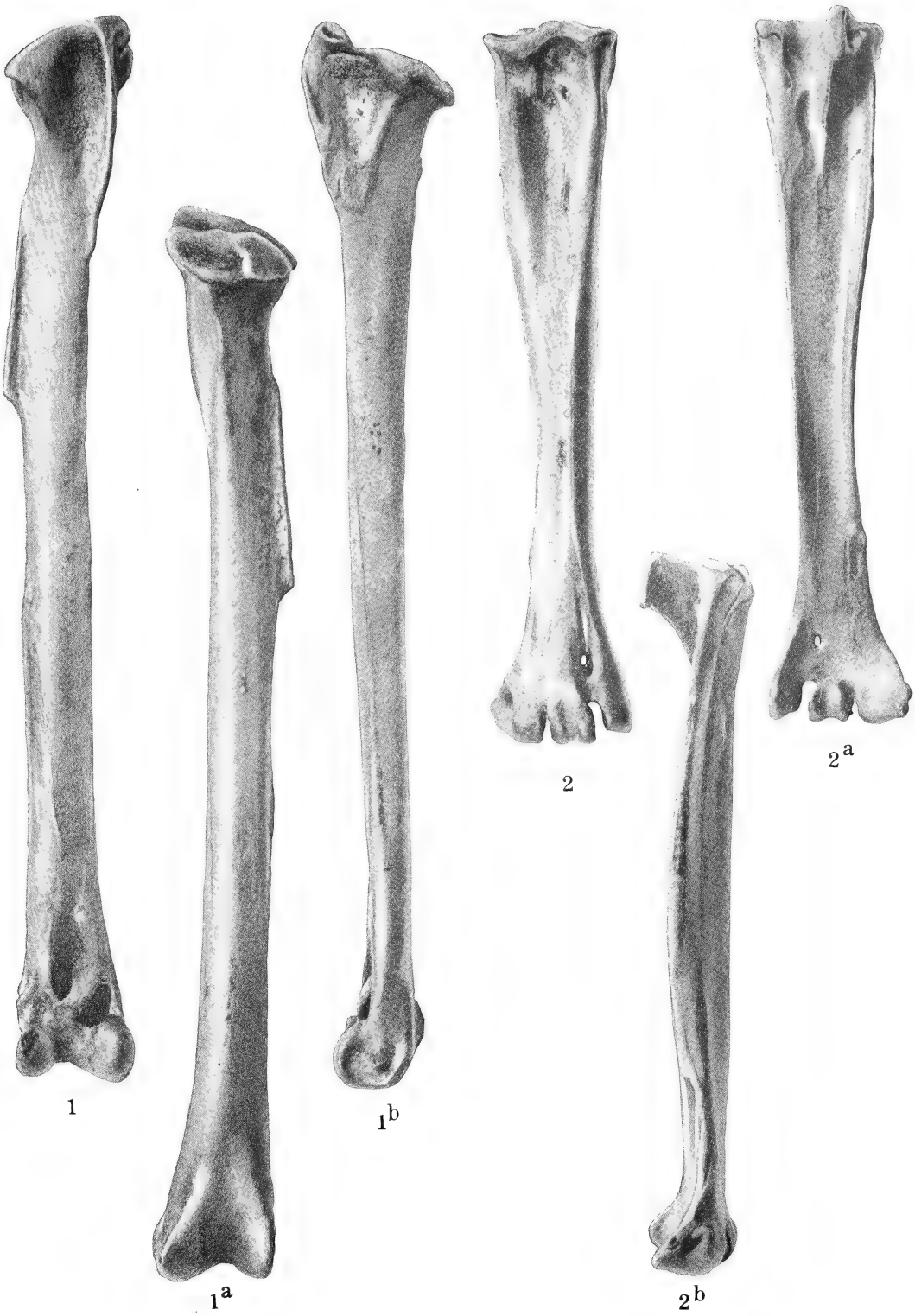
Spizaëtus grinnelli (Miller). Los Angeles Museum Collections.

FIGS. 1, 1a and 1b. Ulna, No. C1937, palmar, external and internal views, × 1.
2 and 2a. Radius, No. D9637, anconal and external views, × 1.



Spizaëtus grinnelli (Miller). Los Angeles Museum Collections.

FIGS. 1 and 1a. Femur, No. C1028, anterior and posterior views, × 1.
2, 2a and 2b. Pelvis, No. C1036, lateral, dorsal and ventral views, × 1.

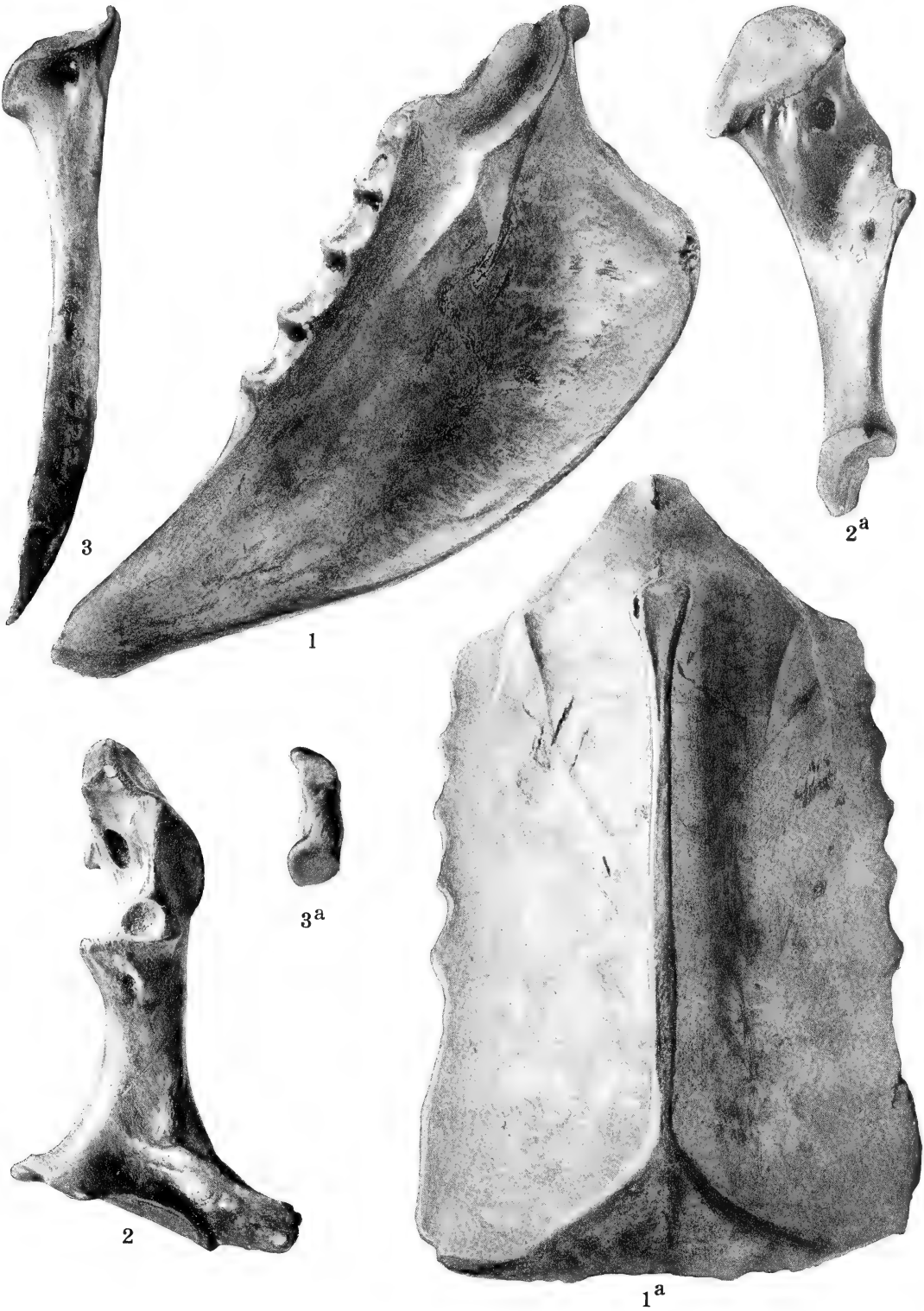


Spizaëtus grinnelli (Miller). Los Angeles Museum Collections.

FIGS. 1, 1a and 1b. Tibiotarsus, No. C3103, anterior, posterior and internal views, × 1.
2, 2a and 2b. Tarsometatarsus, No. C6804, anterior, posterior and internal views, × 1.

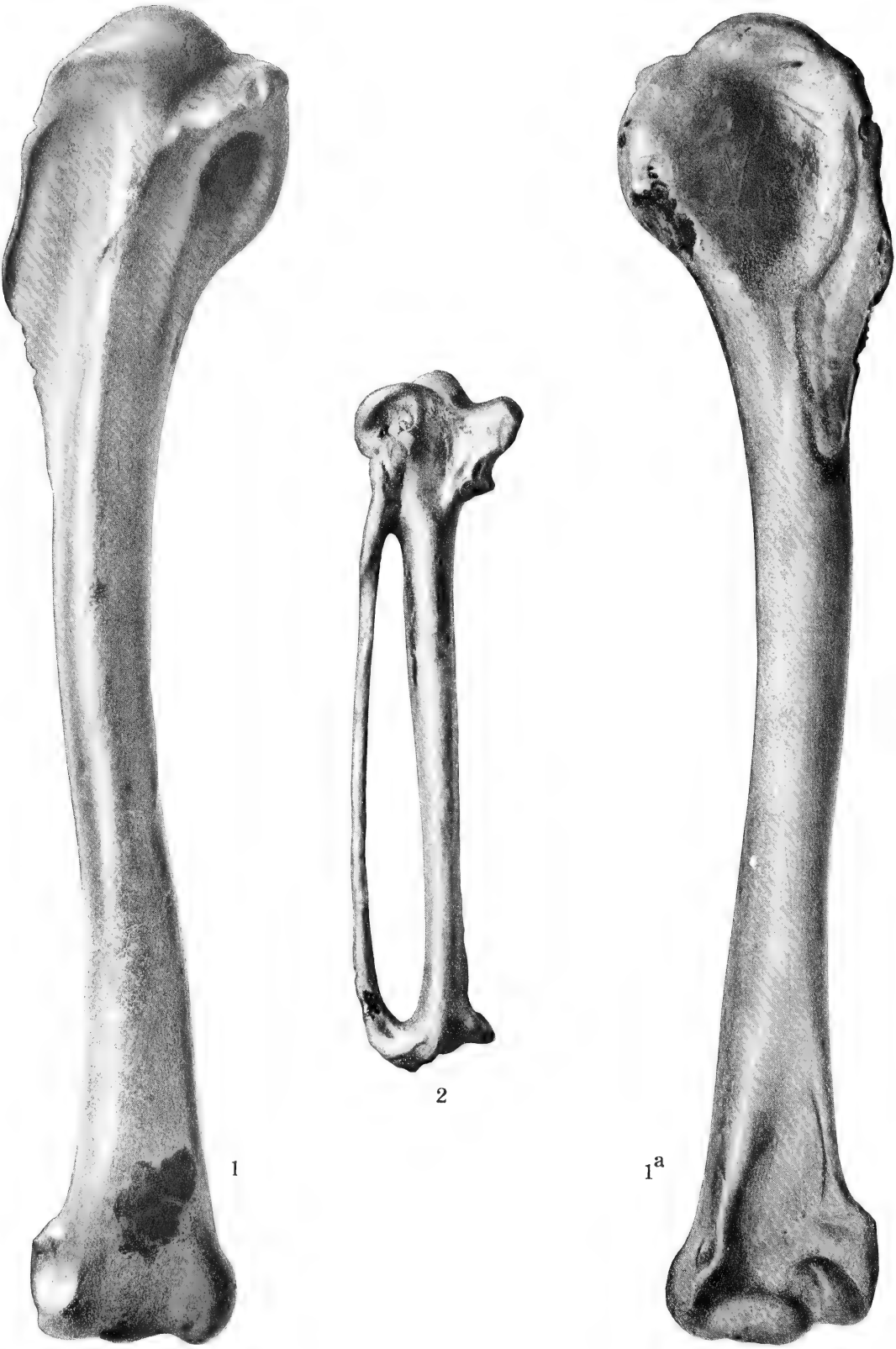
Neogyps errans Miller. Los Angeles Museum Collections.

FIGS. 1 and 1a. Cranium, No. C2053, posterior and lateral views, × 1.
2 and 2a. Rostrum, No. D4615, lateral and ventral views, × 1.
3. Furcula, No. D6522, anterior view, × 1.
3a. Furcula, No. B8633, lateral view, × 1.
4. Mandible, No. C694, dorsal view, × 1.



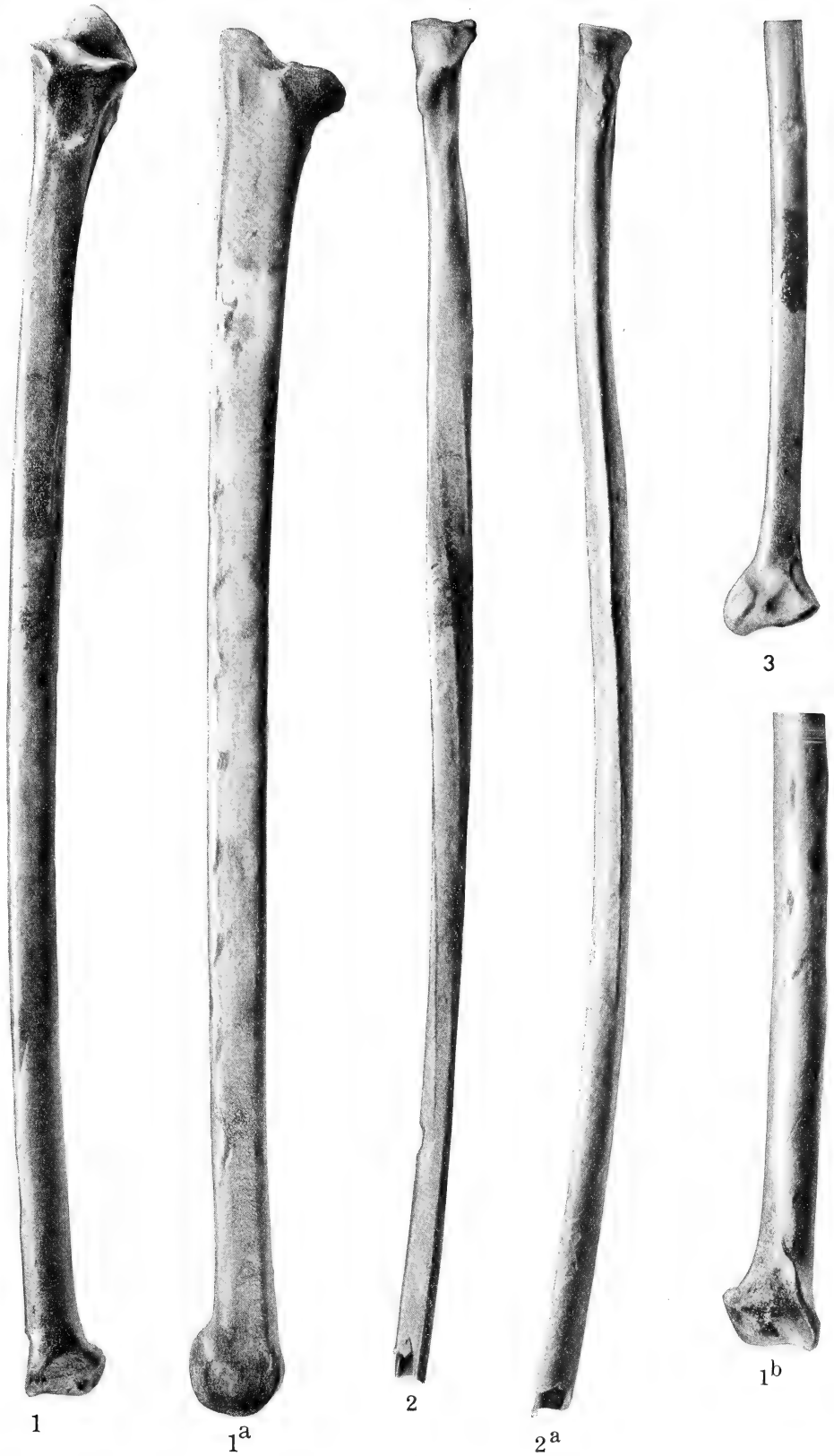
Neogyps errans Miller. Los Angeles Museum Collections.

FIGS. 1 and 1a. Sternum, No. C1118, lateral and ventral views, × 1.
2 and 2a. Coracoid, No. C5467, dorsal and internal views, × 1.
3 and 3a. Scapula, No. C7922, ventral and anterior views, × 1.



Neogyps errans Miller. Los Angeles Museum Collections.

FIGS. 1 and 1a. Humerus, No. C2946, anconal and palmar views, × 1.
2. Carpometacarpus, No. D3374, internal view, × 1.

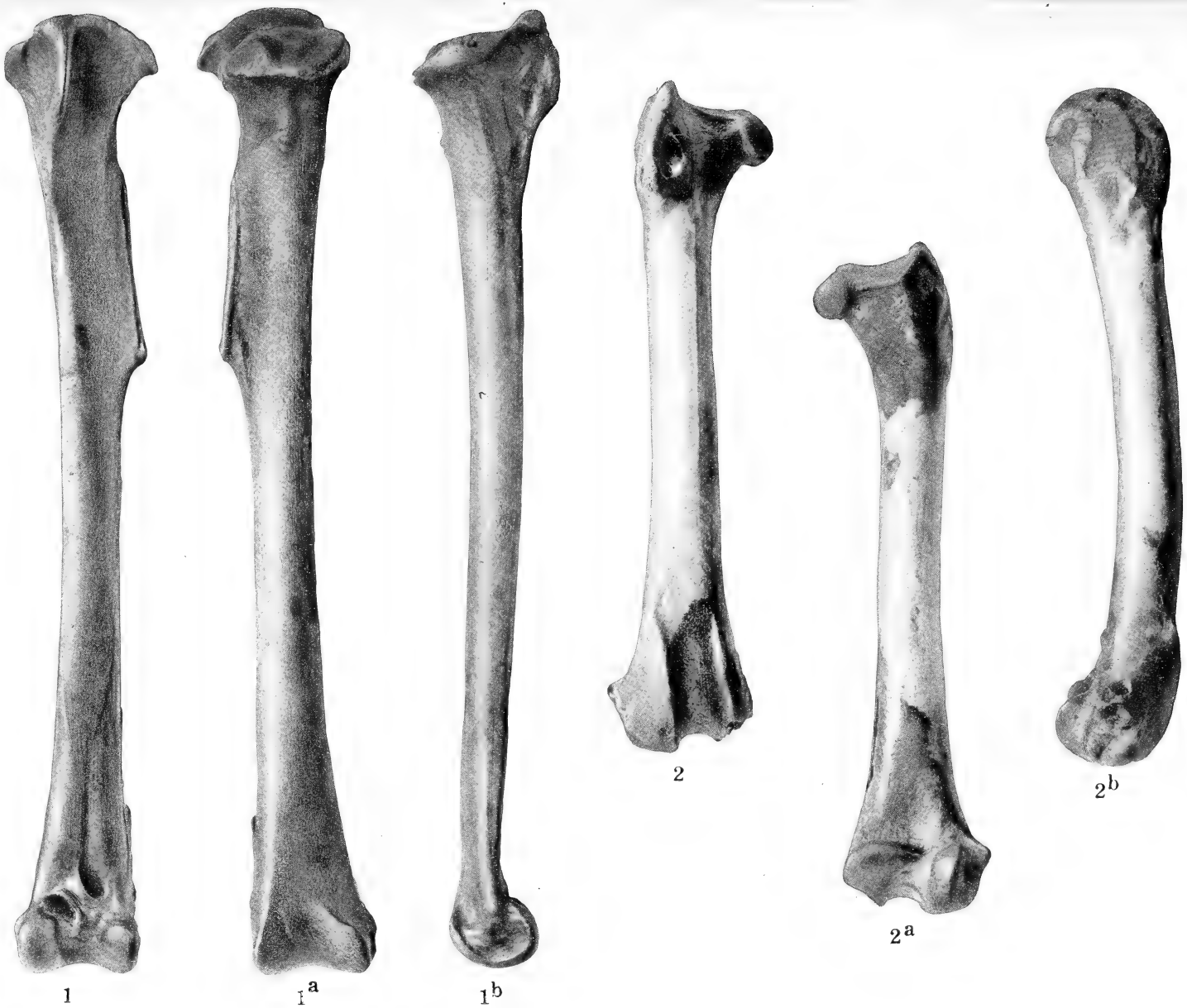


Neogyps errans Miller. Los Angeles Museum Collections.

FIGS. 1 and 1a. Ulna, No. C4049, palmar and external views, × 5/6 approx.
1b. Distal end of ulna, No. C4049, internal view, × 1.
2 and 2a. Proximal end of radius, No. C3849, external and anconal views, × 1.
3. Distal end of radius, No. C1528, anconal view, × 1.

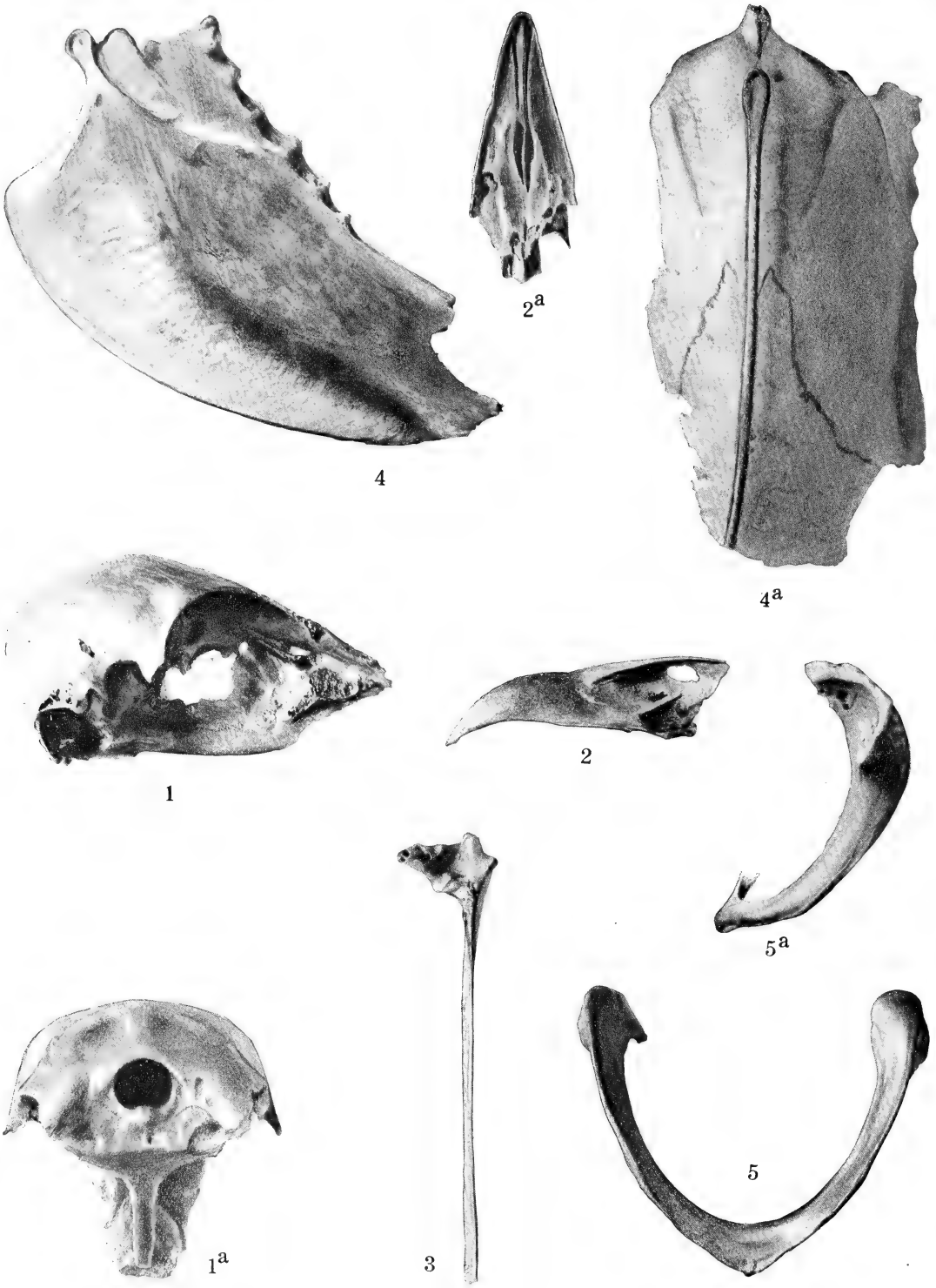
Neogyps errans Miller. Los Angeles Museum Collections.

FIGS. 1, 1a and 1b. Pelvis No. C1314, lateral, dorsal and posterodorsal views, × 1.
2 and 2a. Tarsometatarsus, No. F2017, anterior and posterior views, × 1.



Neogyps errans Miller. Los Angeles Museum Collections.

FIGS. 1, 1a and 1b. Tibiotarsus, No. C4982, anterior, posterior and internal views, × 1.
2, 2a and 2b. Femur, No. J7555, anterior, posterior, and external views, × 1.



Neophrontops americanus Miller. Los Angeles Museum Collections.

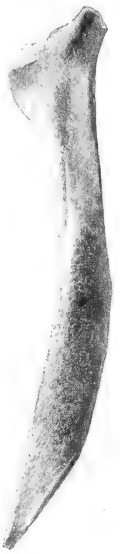
FIGS. 1 and 1a. Cranium, No. D7752, lateral and posteroventral views, × 1.
2 and 2a. Rostrum, No. J9068, lateral and ventral views, × 1.
3. Left ramus of mandible, No. C7398, dorsal view, × 1.
4 and 4a. Sternum, No. E2033, lateral and ventral views, × 1.
5 and 5a. Furcula, No. E3859, anterior and lateral views, × 1.

3

2a

3a

1

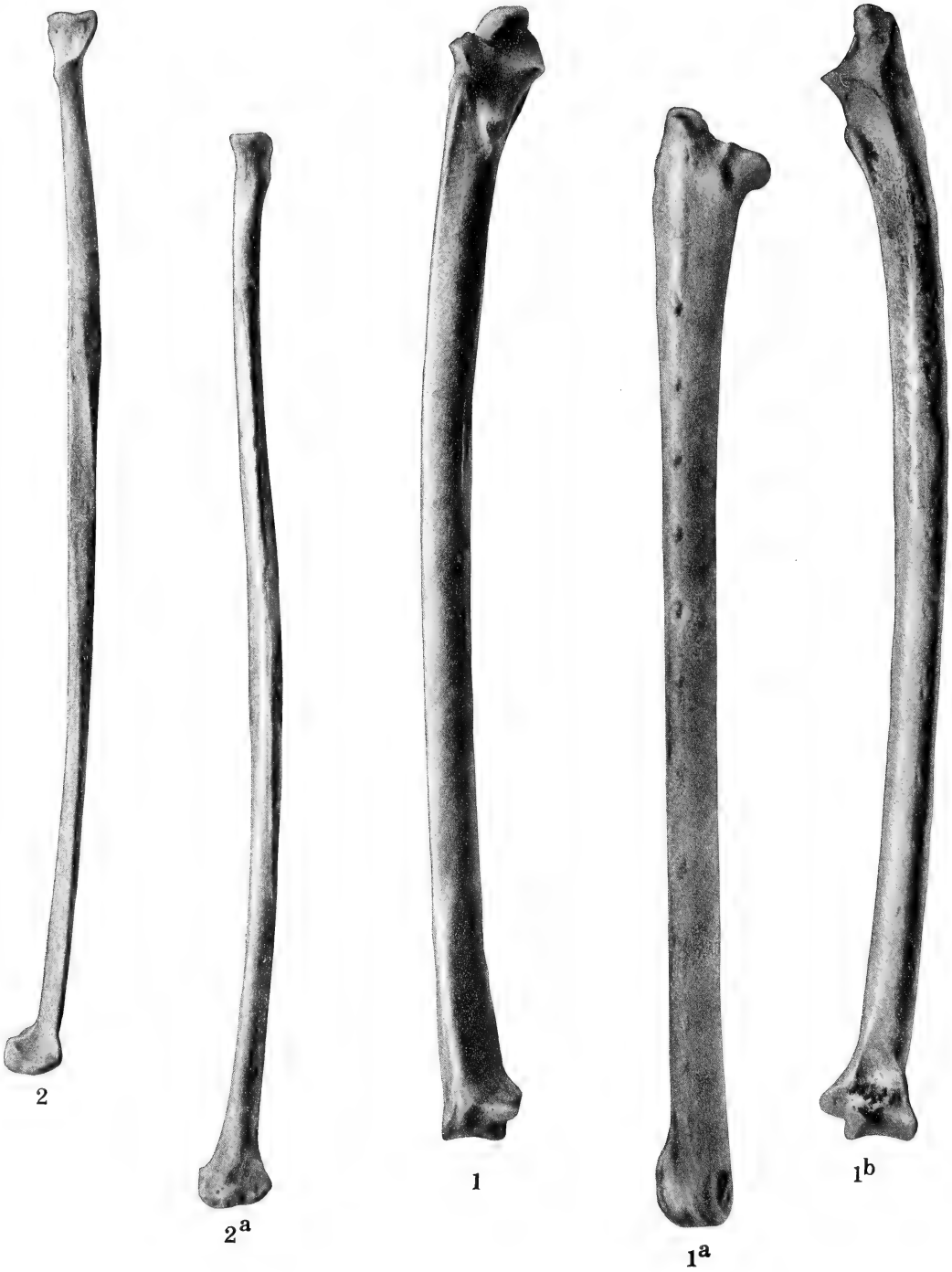


2

4

Neophrontops americanus Miller. Los Angeles Museum Collections.

FIGS. 1. Coracoid, No. E2661, internal view, × 1.
2 and 2a. Scapula, No. E3453, ventral and anterior views, × 1.
3 and 3a. Humerus, No. G1987, palmar and anconal views, × 1.
4. Carpometacarpus, No. H2477, internal view, × 1.



Neophrontops americanus Miller. Los Angeles Museum Collections.

FIGS. 1, 1a and 1b. Ulna, No. D8188, palmar, anconal and internal views, × 1.
2 and 2a. Radius, No. D7841, external and anconal views, × 1.

Neophrontops americanus Miller. Los Angeles Museum Collections.

FIGS. 1 and 1a. Pelvis, No. E2051, lateral and dorsal views, × 1.
2, 2a and 2b. Femur, No. D9765, anterior, posterior and external views, × 1.
3, 3a and 3b. Tibiotarsus, No. F1958, anterior, posterior and internal views, × 1.
4 and 4a. Tarsometatarsus, No. E2159, anterior and posterior views, × 1.